

# Quantifying the per-capita contribution of all components of a migratory cycle: A modelling framework

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## ABSTRACT

Migratory species make use of different habitats and pathways at different life stages, and in different seasons. Ecological management strategies proposed for migratory species should acknowledge the importance of each component of the migratory cycle. Metapopulation approaches used to assess the quality of habitats do not capture key features of migratory populations. In recent years, contribution metrics – roughly, the annual contribution to a population from a single individual – that are suitable for migratory species and quantify the quality of habitats and pathways have been developed. However, existing contribution metrics are either not suitable for use on species that experience complex life histories or movement strategies; or are only able to differentiate between pathways taken during the first season of the annual cycle. Here, we develop a modelling framework to calculate contribution metrics that quantify the contribution of individuals migrating along specific pathways over any number of seasons in the annual cycle. Our framework yields easily-computable formulae, even for population models with complex migratory patterns. We illustrate our framework using hypothetical examples as well as a model inspired by the monarch butterfly, and highlight ecological insights that could not have been found using existing contribution metrics. We envisage our framework being used to identify the most important or vulnerable components of the migratory cycle, such that appropriate conservation strategies may be applied.

## 1. Introduction

Wildlife populations may make use of different habitats at different life stages, and in different seasons. The dynamics of a population over an entire year depend on contributions from each component of the cycle. Contribution metrics, which are derived from a population model, can be used to quantify the importance of each component. Existing contribution metrics quantify the contribution of individuals migrating along a specific pathway in the first season of the annual cycle, or individuals in a specific habitat in the first season of the annual cycle.

Here, we introduce two new metrics that quantify the contribution of individuals migrating along specific pathways over several seasons of the annual cycle. Pathways that include every season describe full migratory routes. So our metrics provide greater insight into how different migratory pathways contribute to the dynamics of the total population.

Migration is a behavioural adaptation that has evolved to cope with seasonal changes to environments. However, many migratory species are suffering serious declines due to environmental and climate change (Huntley et al., 2006; Robinson et al., 2009; Wilcove

and Wikelski, 2008). The conservation of migratory species requires adequate protection across its entire range and careful consideration of factors such as habitat connectivity and migratory bottlenecks (Runge et al., 2014; Weber et al., 1999). The challenge of providing this protection has resulted in IUCN (International Union for Conservation of Nature) targets being met less successfully for migratory species than for sedentary species (Runge et al., 2015).

The conservation of migratory species is important at the ecosystem scale. The life histories of some species are based around the predictable seasonal movements of migrants (Bauer and Hoye, 2014). Migrants also provide a large-scale linking of ecosystems, transporting nutrients, energy and other organisms (Bauer and Hoye, 2014; Wilcove and Wikelski, 2008). The decline of a migratory population can have significant ecological impacts at the level of the population, community and ecosystem (Shuter et al., 2011).

The study of migratory species is usually done on the level of the individual – its choices and their consequences (Bowlin et al., 2010). Contribution metrics allow for migratory species to be studied at the population level. The first contribution metric was developed by Runge

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et al. (2006) using theory from matrix population models; which dates back to the 1940s (Lefkovich, 1965; Leslie, 1945, 1948); see more recently (Caswell, 2001). However, this metric did not account for crucial elements of migratory models such as: seasonality; differences between breeding and non-breeding habitats; and regular movements between habitats (Taylor and Hall, 2012; Wiederholt et al., 2018). Wiederholt et al. (2018) adapted Runge et al.’s metric such that the contribution of an individual to a migratory population can be calculated across a two season annual cycle. This metric was then generalised further by Sample et al. (2019) in order to calculate the contribution of an individual migrating along a specific pathway in the first season of the annual cycle, and to calculate the contribution of individuals that are in a specific habitat in the first season of the annual cycle.

Inspired by the line of inquiry across (Runge et al., 2006; Sample et al., 2019; Wiederholt et al., 2018), the purpose of the present paper is to further generalise contribution metrics in order to calculate the contribution of an individual migrating along specific pathways over any number of seasons in an annual cycle. Indeed, we propose two new so-called pathway contribution metrics for a class of discrete migratory matrix population projection models which are stratified according to stage and habitat. This generalisation allows us to quantify the contribution of full migratory routes, or any sections of the migratory route that may be of interest, perhaps due to migratory bottlenecks (Buler and Moore, 2011; Runge et al., 2014). Our method can be used to calculate contribution metrics for migratory models with any number of seasons, habitats or stages. Furthermore, in certain cases we provide formulae to link our pathway metrics to the habitat metrics in Sample et al. (2019), and to the asymptotic growth rate of the population.

The paper is organised as follows. In Section 2, we gather notation, describe the underlying model, and present our new pathway contribution metrics. The main technical ingredients are linear algebra (matrix) methods. In Section 3, we illustrate the utility of the metrics by applying them to existing models from the literature. In Section 4, we interpret our results and provide summarising remarks. We provide an Appendix containing some technical details and supporting information for the examples.

## 2. Materials and methods

Here we give a detailed account of the construction, analysis and interpretation of our pathway contribution metrics. We begin by introducing the underlying dynamic migratory population model, which we term the *annual cycle model*. We then set out how to calculate pathway contribution metrics from this model and how to average across several stages and habitats. We also elucidate the connection between the new pathway contribution metrics, the existing habitat contribution metrics and the asymptotic growth rate.

### 2.1. Mathematical notation

Here we introduce frequently used operations. We use operations involving Kronecker products,  $\otimes$ , to construct block matrices with particular structures. We use  $E_{n,i,j}$  to denote a  $n \times n$  zero matrix with a one in the  $(i, j)$ th entry, see Table 2.1. Let  $B_i \in \mathbb{R}^{m \times m}$  for all  $i \in \{1, \dots, n\}$ , and let  $b'_{x,y}$  denote the  $(x, y)$ th entry of  $B_i$ . We use the operation:

$$A = \sum_{i=1}^n E_{n,ii} \otimes B_i$$

to construct a block diagonal matrix  $A \in \mathbb{R}^{mn \times mn}$ , with  $n^2$  blocks each of size  $m \times m$ , where the  $(i, i)$ th block is given by  $B_i$ . We use the operation:

$$C = \sum_{i=1}^n B_i \otimes E_{n,ii}$$

to construct a block matrix  $C \in \mathbb{R}^{mn \times mn}$ , with  $m^2$  blocks each of size  $n \times n$ . Each block is a diagonal matrix and, in particular  $b'_{x,y}$  is the  $(i, i)$ th entry of the  $(x, y)$ th block of  $C$ .

**Table 2.1**  
Mathematical notation used.

Symbol	Definition
$\otimes$	Kronecker matrix product
$\circ$	Hadamard (entrywise) matrix product
$\oslash$	Hadamard (entrywise) matrix division
$T$	Transposes a vector or matrix
$\ \cdot\ _1$	One-norm of a vector or matrix
$\mathbb{1}_n$	$n \times 1$ vector of ones
$e_{n,i}$	$n \times 1$ vector of zeros with $i$ th entry equal to one
$E_{n,i,j}$	$n \times n$ zero matrix with $(i, j)$ th entry equal to one
$I_n$	$n \times n$ identity matrix
$J_n$	$n \times n$ matrix of ones

We use  $\oslash$  to denote Hadamard division of vectors, written  $z = y \oslash x$  for vectors  $x$  and  $y$ , and where

$$z_j := \begin{cases} 0, & x_j = 0, \\ \frac{y_j}{x_j}, & \text{otherwise.} \end{cases}$$

Here  $x_j$  and  $y_j$  denote the  $j$ th entries of  $x$  and  $y$ , respectively.

We note that for nonnegative matrices  $A \in \mathbb{R}_+^{p \times m}$  and vectors  $x \in \mathbb{R}_+^m$ , we have

$$\mathbb{1}_p^T A x = \sum_{j=1}^m (Ax)_j = \|Ax\|_1,$$

where  $\|\cdot\|_1$  denotes the usual 1-norm on real Euclidean space. Multiplying a nonnegative matrix on the left by  $\mathbb{1}^T$  returns a row vector composed of the column sums of the matrix.

Finally, for compatibly sized vectors  $x$  and  $y$ , we let

$$\text{row} \left( \begin{bmatrix} x \\ y \end{bmatrix} \right) := [x \quad y]$$

denote the row operation which simply arranges two vectors into one row. We use this operation for wholly presentational reasons, when writing the right hand side of the above is not practicable.

Further mathematical notation is listed in Table 2.1.

### 2.2. The annual cycle model

Here we discuss the underlying migratory population model which is the essential foundation for the various contribution metrics constructed in Section 2.3. All mathematical notation used is recorded in Tables 2.1 and 2.2.

The so-called annual cycle model borrows theory from matrix population models and source–sink models (see, for example, Caswell, 2001; Cushing, 1998 and Pulliam, 1988, respectively), so that matrix entries contain information based on demographic rates and movement rates, the latter between discrete habitats or patches. The model may be visualised as a network, where nodes represent habitats and edges represent migration pathways, as is done in Sample et al. (2018) and Taylor and Hall (2012).

The annual cycle model is particularly inspired by the models appearing in Hunter and Caswell (2005) and Sample et al. (2019). A key novel feature of the present model is the introduction of the so-called seasonal survival matrices (see (2.7)). As shall be explained in due course, these matrices can be used to highlight pathways of interest and allow managers to gain more insight into the important factors across the whole annual cycle.

We provide details of the annual cycle model, which stratifies the population of interest by stage structure and spatial location (or habitat). We assume there are  $c$  stages, and  $n$  habitats. We define an annual cycle matrix  $A$  that projects a population over an annual cycle from a fixed anniversary season. The annual cycle matrix contains the demographic update information associated with habitats, as well as

**Table 2.2**  
Symbols used for parameters and matrices in the annual cycle model.

Symbol	Definition
$c$	Number of population stages
$n$	Number of habitat patches
$s$	Number of seasons in the annual cycle
$t$	Discrete time variable (years)
$\mathcal{A}$	$cn \times cn$ annual cycle matrix that projects the population over one time step
$\mathbf{x}(t)$	$cn \times 1$ vector of the population distribution at the start of annual cycle $t$ , with $n$ subvectors denoted by $\mathbf{x}_j(t)$
$\mathbf{x}_j(t)$	$c \times 1$ vector of the population stage distribution in habitat $j$ at the start of annual cycle $t$
$x_j^i(t)$	Number of individuals in stage $i$ and habitat $j$ at the start of annual cycle $t$
$A_k$	$cn \times cn$ seasonal matrix that projects the population over season $k$ , $A_k := \mathbb{D}_k \mathbb{M}_k$
$D_{j,k}$	$c \times c$ demographic projection matrix for habitat $j$ in season $k$
$M_k^i$	$n \times n$ migration projection matrix for stage $i$ in season $k$ , contains the probability that an individual in stage $i$ migrates along a pathway in season $k$ and survives
$\mathbb{D}_k$	$cn \times cn$ block matrix containing the demographic update information for all habitats in season $k$
$\mathbb{M}_k$	$cn \times cn$ block matrix containing the migration update information for all stages in season $k$
$\mathbb{P}_k$	$cn \times cn$ block matrix containing the probability that an individual migrates along a pathway in season $k$ , for all stages
$P_k^i$	$n \times n$ matrix containing the probability that an individual in stage $i$ migrates along a pathway in season $k$
$\mathbb{S}_k$	$cn \times cn$ block matrix containing the survival probability of migrating along a pathway in season $k$ , for all stages
$S_k^i$	$n \times n$ matrix containing the probability that an individual in stage $i$ survives migration along a pathway in season $k$
$\hat{A}_k$	$cn \times cn$ seasonal survival matrix that contains the survival probability of migration along pathways and demographic rates for season $k$ ; probability that an individual migrates along pathways is not included, $\hat{A}_k := \mathbb{D}_k \mathbb{S}_k$

the migration update information associated with migration pathways. Thus, the underlying discrete-time annual cycle model is given by

$$\mathbf{x}(t+1) = \mathcal{A}\mathbf{x}(t) \quad t = 0, 1, 2, \dots, \quad \mathbf{x}(0) = \mathbf{x}^0, \quad (2.1)$$

where  $\mathcal{A} \in \mathbb{R}_+^{cn \times cn}$  is the annual cycle matrix, and  $\mathbf{x}(t) \in \mathbb{R}_+^{cn}$  is the structured population at (annual) time-step  $t$ , recorded during the anniversary season. The vector  $\mathbf{x}^0$  models the initial population distribution. The asymptotic growth rate,  $\lambda$ , of the population is well-known to be given by the dominant eigenvalue of  $\mathcal{A}$  (equal to the spectral radius of  $\mathcal{A}$ ). The quantity  $\lambda$  describes the asymptotic behaviour of (nonzero) solutions of (2.1).

The spatial structure encoded in  $\mathcal{A}$  and  $\mathbf{x}(t)$  can be decomposed into  $n^2$  blocks and  $n$  subvectors, respectively, by writing

$$\mathcal{A} = \begin{pmatrix} (\mathcal{A})_{11} & \cdots & (\mathcal{A})_{1n} \\ \vdots & \ddots & \vdots \\ (\mathcal{A})_{n1} & \cdots & (\mathcal{A})_{nn} \end{pmatrix} \quad \text{and} \quad \mathbf{x}(t) = \begin{pmatrix} \mathbf{x}_1(t) \\ \vdots \\ \mathbf{x}_n(t) \end{pmatrix}.$$

Here,  $(\mathcal{A})_{ij} \in \mathbb{R}_+^{c \times c}$  is the population projection matrix for the subpopulation that starts the annual cycle in habitat  $j$  and is in habitat  $i$  at the end of the annual cycle; and,  $\mathbf{x}_j(t) \in \mathbb{R}_+^c$  represents the stage distribution within habitat  $j$  at the start of the annual cycle (and at time-step  $t$ ). Each  $\mathbf{x}_j(t)$  is a vector of the form

$$\mathbf{x}_j(t) = \begin{pmatrix} x_j^1(t) \\ \vdots \\ x_j^c(t) \end{pmatrix},$$

where  $x_j^i(t)$  denotes the number of individuals in stage  $i$  and habitat  $j$  at the start of the annual cycle.

The life rates experienced by a migratory population depend on the season. Hence, the annual cycle is decomposed into  $s$  seasons, each of which is assigned a label  $k \in \{1, \dots, s\}$ , such that the anniversary season is season 1 and consecutive seasons are assigned consecutive numbers. The term season is used somewhat loosely, and is essentially a division of the annual cycle into smaller units of time.

Thus, the annual cycle matrix,  $\mathcal{A}$ , is in fact constructed by taking the product of  $s$  seasonal matrices,  $A_k \in \mathbb{R}_+^{cn \times cn}$ , via left multiplication. That is,

$$\mathcal{A} := \prod_{k=1}^s A_k = A_s \cdots A_2 A_1. \quad (2.2)$$

The biological interpretation of each element of the seasonal matrices is hard to infer owing to the demographic and migration information being entangled. We define  $D_{j,k} \in \mathbb{R}_+^{c \times c}$  to be the demographic projection matrix associated with habitat  $j$  in season  $k$ , and let  $d_{xy}$  denote the

$(x, y)$ th entry of  $D_{j,k}$ . Each  $d_{xy}$  term is assumed to be linear and constant in time and quantifies the survival, growth, or fecundity of stage  $y$ . In other words,  $d_{xy}$  represents the number of individuals in stage  $x$  generated from an individual in stage  $y$  and habitat  $j$ , during season  $k$ . Furthermore, we define  $M_k^i \in \mathbb{R}_+^{n \times n}$  to be the migration projection matrix associated with stage  $i$  in season  $k$ , and let  $m_{xy}$  denote the  $(x, y)$ th entry of  $M_k^i$ . Each  $m_{xy}$  term represents the probability that an individual in stage  $i$  migrates from habitat  $y$  to  $x$  and survives, during season  $k$ .

Inspired by Sample et al. (2019), we use Kronecker products,  $\otimes$ , to construct two block matrices. One of these matrices,  $\mathbb{D}_k \in \mathbb{R}_+^{cn \times cn}$ , contains the demographic update information for the total population in season  $k$ ; whilst the other,  $\mathbb{M}_k \in \mathbb{R}_+^{cn \times cn}$ , contains the migration update information for the total population in season  $k$ . We define  $\mathbb{D}_k$  and  $\mathbb{M}_k$  by,

$$\mathbb{D}_k := \sum_{j=1}^n E_{n,jj} \otimes D_{j,k} \quad \text{and} \quad \mathbb{M}_k := \sum_{i=1}^c M_k^i \otimes E_{c,ii}, \quad (2.3)$$

where, recall,  $E_{n,ii}$  is a  $n \times n$  matrix of zeros, apart from a one in the  $(i, i)$ th entry. The construction of  $\mathbb{D}_k$  results in a block diagonal matrix where the  $(j, j)$ th block is given by  $D_{j,k}$ . Whilst, the construction of  $\mathbb{M}_k$  results in a block matrix, where each block is a diagonal matrix and  $m_{xy}$  of  $M_k^i$  is the  $(i, i)$ th term of the  $(x, y)$ th block of  $\mathbb{M}_k$ , see Section 2.1.

When constructing the seasonal matrices,  $A_k \in \mathbb{R}_+^{cn \times cn}$ , we assume that, within a season, migration is followed by demography. Hence,

$$A_k := \mathbb{D}_k \mathbb{M}_k \quad k \in \{1, \dots, s\}. \quad (2.4)$$

The upshot of the above construction is that the seasonal matrices can also be decomposed into  $n^2$  blocks, namely

$$A_k = \begin{pmatrix} (A_k)_{11} & \cdots & (A_k)_{1n} \\ \vdots & \ddots & \vdots \\ (A_k)_{n1} & \cdots & (A_k)_{nn} \end{pmatrix},$$

where,  $(A_k)_{ij} \in \mathbb{R}_+^{c \times c}$  is the population projection matrix for the subpopulation that moves from habitat  $j$  to habitat  $i$  during season  $k$ .

The migration update information contains information about the proportion of individuals migrating and the survival probability associated with the migration. We impose additional structure on the entries  $m_{xy}$  of the migratory matrices  $M_k^i$ . Specifically, we assume that

$$m_{xy} = p_{xy} \times s_{xy} \quad \text{for all } x, y,$$

where  $p_{xy}$  represents the probability that an individual in stage  $i$  migrates from habitat  $y$  to  $x$ , in season  $k$ , and  $s_{xy}$  represents the migratory survival probability for an individual in stage  $i$  that migrates from

habitat  $y$  to  $x$ , in season  $k$ . Then, letting  $P_k^i \in \mathbb{R}_+^{n \times n}$  and  $S_k^i \in \mathbb{R}_+^{n \times n}$  have respective components  $p_{xy}$  and  $s_{xy}$ , it follows that  $P_k^i$  and  $S_k^i$  contain the proportion of stage  $i$  individuals that migrate in season  $k$ , and the survival probability of stage  $i$  individuals during migration in season  $k$ , respectively.

Moreover, defining

$$\mathbb{P}_k := \sum_{i=1}^c P_k^i \otimes E_{c,ii} \quad \text{and} \quad \mathbb{S}_k := \sum_{i=1}^c S_k^i \otimes E_{c,ii}, \quad (2.5)$$

a routine calculation shows that  $\mathbb{M}_k$ ,  $\mathbb{S}_k$  and  $\mathbb{P}_k$  are related by

$$\mathbb{M}_k = \mathbb{P}_k \circ \mathbb{S}_k \quad \text{for all } k. \quad (2.6)$$

We define seasonal survival matrices,  $\hat{A}_k \in \mathbb{R}_+^{cn \times cn}$ , by

$$\hat{A}_k := \mathbb{D}_k \mathbb{S}_k \quad k \in \{1, \dots, s\}. \quad (2.7)$$

These matrices encode the migratory survival and demographic rates, but, unlike  $A_k$ , do not include the probability that migration along a pathway occurs. Hence, each block,  $(\hat{A}_k)_{xy} \in \mathbb{R}_+^{c \times c}$ , may be interpreted as the population projection matrix if the whole population migrates from habitat  $y$  to habitat  $x$  during season  $k$ .

It is shown in Appendix A that, for every  $k$ ,

$$(A_k)_{xy} = (\hat{A}_k)_{xy} (\mathbb{P}_k)_{xy}. \quad (2.8)$$

Here  $(A)_{xy}$  represents the  $(x, y)$ th block of  $A$ .

We conclude the subsection by providing further commentary on features of the annual cycle model.

First, we note that the above annual cycle model is equivalent to that in Sample et al. (2019), up to the use of transposes, and that our construction results in the sub-blocks of the vectors and matrices being arranged by habitat. It is also possible to construct the seasonal matrices using the vec-permutation approach, as is done in Hunter and Caswell (2005). The seasonal survival matrices  $\hat{A}_k$  in (2.7) are a novel feature of the present work. The model may also be constructed for the setting where demography is assumed to be followed by migration during each season, meaning (2.4) is replaced by  $A_k = \mathbb{M}_k \mathbb{D}_k$  and (2.7) is replaced by  $\hat{A}_k = \mathbb{S}_k \mathbb{D}_k$  for every  $k$ ; this would change the results both qualitatively and quantitatively, but the construction of the contribution metrics in Section 2.3 remains the same.

Second, the choice of which season is taken as the anniversary season determines the order in which the seasonal matrices are multiplied, and is a choice for the modeller. Cyclic permutations of the seasonal matrices do not alter the dominant eigenvalue,  $\lambda$ , of the annual cycle matrix,  $\mathcal{A}$ , as the nonzero eigenvalues of products of matrices are equal; see Horn and Johnson (1990, Theorem 1.3.22) or Caswell (2001, p.350). In other words, the asymptotic growth rate of the population,  $\lambda$ , is independent of the choice of anniversary season, as one would expect. However, cyclic permutations of the seasonal matrices may alter the corresponding eigenvectors. Indeed, since  $\mathcal{A}$  is componentwise nonnegative, it has a right eigenvector corresponding to  $\lambda$  which may be chosen to be componentwise nonnegative; see, for example, Berman and Plemmons (1994, Theorem 1.1, p.26). This eigenvector is often called the *stable stage structure* of  $\mathcal{A}$ . Under reasonable ecological assumptions, such as  $\mathcal{A}$  being irreducible, then  $\lambda$  is a simple eigenvalue by the Perron-Frobenius Theorem (Berman and Plemmons, 1994, Theorem 1.4, p.27) and, the stable stage structure is unique up to multiplication by a constant. We comment that the stable stage structure will, in general, depend on the choice of anniversary season, but the stable stage structure does not play a large role in the present work.

Finally, we comment on incorporating inter-annual variations into the annual cycle model. One generalisation of the annual cycle model described here is to allow the seasonal vital rates to depend on the year,  $t$ , resulting in each seasonal matrix  $A_k$  (and therefore  $\mathcal{A}$ ) also depending on  $t$ . Alternatively, if a population experiences inter-annual variations which are periodic over multiple years, then the ‘‘annual’’

cycle matrix  $\mathcal{A}$  could be expanded to span the required number of years. This again produces a ‘‘time-invariant’’ model of the form (2.1), at the cost of losing track of annual variations in the population. However, in the present work, we are most interested in transient dynamics, via pathway contribution metrics, that are calculated over one annual cycle. Thus, for simplicity, we do not include notation that keeps record of the year.

### 2.3. Pathway contribution metrics

Here we introduce two new pathway contribution metrics for the annual cycle model presented in Section 2.2. Our metrics generalise those introduced in Sample et al. (2019) and Wiederholt et al. (2018). The connection between our new metrics and these is discussed in Appendix B and Example 3.1. A summary of notation introduced is recorded in Tables 2.3 and 2.4.

Pathway contribution metrics calculate the per capita contribution to the total population of an individual that has travelled along a specific migratory route during the annual cycle. In words, a pathway is the migration an individual takes between one habitat and another (or itself) during a season; a migratory route consists of all pathways that an individual migrates along in an annual cycle.

To describe migratory routes mathematically, we define a vector  $\mathcal{P} \in \mathbb{R}_+^{s+1}$  such that the migratory route is given by

$$\mathcal{P}(1) \rightarrow \mathcal{P}(2) \rightarrow \mathcal{P}(3) \rightarrow \dots \rightarrow \mathcal{P}(s) \rightarrow \mathcal{P}(s+1).$$

Here,  $\mathcal{P}(k) \in \{0, 1, \dots, n\}$  denotes the habitat in which the subpopulation starts in season  $k$  (and ends in season  $k-1$ ). If  $\mathcal{P}(k) = 0$ , then the habitat is unspecified. In this case, the migratory route includes all habitats at the start of season  $k$ .

The pathway that an individual of interest migrates along during season  $k$  is specified by  $\mathcal{P}(k)$  and  $\mathcal{P}(k+1)$ . Define  $\phi \in \{0, 1, \dots, s\}$  to be the number of seasons for which a pathway is specified, and let  $\Phi \in \mathbb{R}^\phi$  store the labels of these seasons. Arrows ( $\rightarrow$ ) are used to indicate the migration within a season with a specified pathway ( $k \in \Phi$ ); whilst crossed arrows ( $\nrightarrow$ ) are used to indicate seasons for which a pathway is not specified ( $k \notin \Phi$ ). If  $k \in \Phi$ , set  $\mathcal{P}(k) = j \in \{1, \dots, n\}$  and  $\mathcal{P}(k+1) = l \in \{1, \dots, n\}$  to track the subpopulation that travels from habitat  $j$  to habitat  $l$  during season  $k$ . Setting  $\mathcal{P}(k) = \mathcal{P}(k+1) = j \neq 0$ , tracks the subpopulation that remains resident in habitat  $j$  during season  $k$ . If  $\mathcal{P}(k) = \mathcal{P}(k+1) = 0$ , then all subpopulations are tracked in season  $k$ .

To calculate pathway contribution metrics, similarly to Sample et al. (2019, Eq. (8)), we take the one-norm of a product of  $s$  matrices. However, when a pathway is specified in season  $k$  we use a function of  $A_k$ , so that only the focal subpopulation is tracked. Our construction focuses solely on the proportion of the subpopulation that migrates on the given pathway.

We introduce

$$A_k := \begin{cases} \hat{A}_k \circ (E_{n, \mathcal{P}(k+1)\mathcal{P}(k)} \otimes J_c), & k \in \Phi, \\ A_k, & \text{otherwise,} \end{cases} \quad (2.9)$$

where  $\hat{A}_k \circ (E_{n, \mathcal{P}(k+1)\mathcal{P}(k)} \otimes J_c)$  is a  $cn \times cn$  matrix which, by construction, has the  $(\mathcal{P}(k+1), \mathcal{P}(k))$ th block equal to the  $(\mathcal{P}(k+1), \mathcal{P}(k))$ th block of  $\hat{A}_k$ , and all other blocks are equal to zero. In other words,  $\hat{A}_k \circ (E_{n, \mathcal{P}(k+1)\mathcal{P}(k)} \otimes J_c)$  only stores the seasonal survival matrix for the subpopulation travelling along the pathway specified in season  $k$ .

The population is projected over the annual cycle, from season 1, by taking the product of all  $A_k$  via left multiplication. Therefore, the annual population projection matrix in the annual cycle model for migratory route  $\mathcal{P}$  is equal to

$$\prod_{k=1}^s A_k = A_s \cdots A_2 A_1. \quad (2.10)$$

In words, if a particular pathway, from habitat  $l$  to  $j$ , is being tracked during a season  $k \in \{1, \dots, s\}$ , then the  $k$ th term in the product is given

**Table 2.3**  
Symbols used to define pathways, migratory routes and contribution metrics.

Symbol	Definition
$\mathcal{P}$	$(s + 1) \times 1$ vector containing the migratory route (sequence of migratory pathways) taken by the focal subpopulation across the annual cycle where $\mathcal{P}(k)$ denotes the habitat in which the focal subpopulation starts season $k$
$\phi$	Number of seasons for which a pathway is specified
$\Phi$	$\phi \times 1$ vector containing the labels of seasons with a specified pathway
$A_k$	$cn \times cn$ matrix that projects the population over season $k$ ; the population migrates along the pathway specified by $\mathcal{P}(k)$ and $\mathcal{P}(k + 1)$ in season $k$
$P_k$	$cn \times cn$ matrix containing the probability that an individual migrates along the pathway, specified by $\mathcal{P}(k)$ and $\mathcal{P}(k + 1)$ , where $k \in \Phi$ , in season $k$
$\gamma$	The number of distinct migratory routes for a specified $\Phi$
$a$	The number of entries in $\Phi$ for which $\Phi(i) + 1 \notin \Phi$
$\mathbb{P}_i$	$cn \times cn$ matrix containing the proportion of individuals travelling a migratory route $\mathcal{P}_i$

**Table 2.4**  
Summary of contribution metrics. Here  $i \in \{1, 2, \dots, c\}$ ,  $j \in \{1, 2, \dots, n\}$  and  $\mathcal{P}$  indicates the migratory route.

Symbol	Type of contribution metric	Equation
$C(\mathcal{P})$	$1 \times cn$ vector of subpopulation pathway contribution metrics, with entries $C_j^i(\mathcal{P})$ ,	(2.11)
$\tilde{C}(\mathcal{P})$	$1 \times cn$ vector of metapopulation pathway contribution metrics, with entries $\tilde{C}_j^i(\mathcal{P})$ ,	(2.12)
$C$	$1 \times cn$ vector of habitat contribution metrics, with entries $C_j^i$	(2.13)

by  $(\hat{A}_k \circ (E_{n,jl} \otimes J_c))$ . Otherwise, if no particular pathway is specified during season  $k$ , the  $k$ th term is given by the seasonal matrix  $A_k$ . Consecutive seasons with specified pathways must be defined such that

$$(\hat{A}_{k+1} \circ (E_{n,ml} \otimes J_c))(\hat{A}_k \circ (E_{n,jh} \otimes J_c)), \quad j = l.$$

Here,  $m, l, j, h \in \{1, \dots, n\}$  denote habitats and the pathway from habitat  $h$  to  $j$  is tracked during season  $k$ , whilst the pathway from  $l$  to  $m$  is tracked during the following season  $(k + 1)$ . To be a valid migratory route,  $j$  and  $l$  must correspond to the same habitat, that is  $j = l$ . Otherwise, the matrix product is zero, as it contains an impossible migratory route. Furthermore, if  $k \notin \Phi$ , but  $k - 1 \in \Phi$  and  $k + 1 \in \Phi$ , then  $\mathcal{P}(k)$  and  $\mathcal{P}(k + 1)$  will be nonzero, despite season  $k$  not being labelled as a season with a specified pathway. In this situation, where  $k$  is not a season with a specified pathway, the  $(\mathcal{P}(k + 1), \mathcal{P}(k))$ th block of  $A_k$  is picked up in (2.10). Alternatively, if  $k$  is a season with a specified pathway, then the  $(\mathcal{P}(k + 1), \mathcal{P}(k))$ th block of  $\hat{A}_k$  is picked up in (2.10). Later, we provide an illustrative example to highlight this point, see Example 2.3.

We are now in position to define two types of pathway contribution metric. First, for a given migratory route  $\mathcal{P}$ , we define  $C(\mathcal{P})$  by

$$C(\mathcal{P}) := \mathbb{1}_{cn}^T \prod_{k=1}^s A_k = \mathbb{1}_{cn}^T A_s \cdots A_2 A_1$$

$$= [C_1^1(\mathcal{P}) \quad \cdots \quad C_1^c(\mathcal{P}) \quad | \quad \cdots \quad | \quad C_n^1(\mathcal{P}) \quad \cdots \quad C_n^c(\mathcal{P})]. \quad (2.11)$$

Here  $C_j^i(\mathcal{P})$  is the per capita contribution of an individual that starts the annual cycle in stage  $i$  and habitat  $j$  and migrates along  $\mathcal{P}$ , to the subpopulation that migrates along  $\mathcal{P}$ . We call  $C(\mathcal{P})$  the *subpopulation pathway contribution metrics*.

The second pathway contribution metric,  $\tilde{C}(\mathcal{P})$ , is defined by

$$\tilde{C}(\mathcal{P}) := \mathbb{1}_{cn}^T \prod_{k=1}^s A_k P_k = \mathbb{1}_{cn}^T A_s P_s \cdots A_2 P_2 A_1 P_1$$

$$= [\tilde{C}_1^1(\mathcal{P}) \quad \cdots \quad \tilde{C}_1^c(\mathcal{P}) \quad | \quad \cdots \quad | \quad \tilde{C}_n^1(\mathcal{P}) \quad \cdots \quad \tilde{C}_n^c(\mathcal{P})]. \quad (2.12)$$

Here  $\tilde{C}_j^i(\mathcal{P})$  is the per capita contribution of an individual that starts the annual cycle in stage  $i$  and habitat  $j$  and travels along the migratory route  $\mathcal{P}$ , to the total population. We call  $\tilde{C}(\mathcal{P})$  the *metapopulation pathway contribution metrics*. Also,  $P_k$  is given by

$$P_k := \begin{cases} I_n \otimes (\mathbb{P}_k)_{\mathcal{P}(k+1), \mathcal{P}(k)}, & k \in \Phi, \\ I_{cn}, & \text{otherwise,} \end{cases}$$

where  $I_n \otimes (\mathbb{P}_k)_{\mathcal{P}(k+1), \mathcal{P}(k)}$  is a  $cn \times cn$  matrix with the  $(\mathcal{P}(k + 1), \mathcal{P}(k))$ th block of  $\mathbb{P}_k$  along the diagonal. Therefore, due to the construction of

$A_k$  and  $P_k$ , and recalling the relationship (2.8), gives

$$A_k P_k = \begin{cases} A_k \circ (E_{n, \mathcal{P}(k+1)\mathcal{P}(k)} \otimes J_c), & k \in \Phi, \\ A_k, & \text{otherwise.} \end{cases}$$

The key difference between the subpopulation pathway contribution metrics and metapopulation pathway contribution metrics, is that  $C(\mathcal{P})$  does not account for the proportion of the population migrating along  $\mathcal{P}$  whereas,  $\tilde{C}(\mathcal{P})$  does account for the proportion of the population migrating along  $\mathcal{P}$ . Consequently,  $\tilde{C}(\mathcal{P}) \leq C(\mathcal{P})$  (componentwise inequality) due to the construction of  $\tilde{C}(\mathcal{P})$  as, in each season where there is a choice of pathway, the fraction of the total population that migrates along  $\mathcal{P}$ , in general, becomes smaller.

We define a *full migratory route* to be a migratory route where every season in the annual cycle has a specified pathway; that is,  $A_k = \hat{A}_k \circ (E_{n, \mathcal{P}(k+1)\mathcal{P}(k)} \otimes J_c)$  for all  $k$ .

Conversely, if no seasons have specified pathways, that is  $\mathcal{P}_0 := 0 \not\rightarrow 0 \not\rightarrow \cdots \not\rightarrow 0 \not\rightarrow 0$ , then the resulting pathway contribution metric is

$$\tilde{C}(\mathcal{P}_0) := \mathbb{1}^T (A_s I_{cn} \cdots A_k I_{cn} \cdots A_2 I_{cn} A_1 I_{cn})$$

$$= \mathbb{1}^T (A_s \cdots A_k \cdots A_2 A_1) =: C(\mathcal{P}_0) = \mathbb{1}^T A. \quad (2.13)$$

So,  $C(\mathcal{P}_0)$  contains the *habitat contribution metrics* defined in Sample et al. (2019) which, in the present framework, we recover as a special case of a pathway contribution metric. We denote the habitat contribution metrics by  $C$  and denote each entry by  $C_j^i$  and name these the *state contribution metrics*. The state contribution metric  $C_j^i$  can be thought of as the number of individuals (across the total population) that are generated over an annual cycle by an individual that is initially in stage  $i$  and habitat  $j$ .

A summary of the contribution metrics introduced is contained in Table 2.4.

### 2.4. Illustrative examples

Our formulation of pathway contribution metrics in (2.9)–(2.12) is general and allows pathways to be specified in any season. To draw out the key ideas from the mathematical notation, in this section we present some illustrative numerical and general examples.

**Example 2.1.** Consider an annual cycle model with two seasons, two habitats and two stages ( $s = 2, n = 2, c = 2$ ). We use the Hypothetical Metapopulation in Sample et al. (2019, Section 3.1); it represents partial migration between a higher quality habitat (habitat 1) and a lower quality habitat (habitat 2). There is a resident population in both habitats, and migration can occur between habitats in both seasons. The demographic rates used are the same as those from Sample

et al. (2019, Section 3.1) and we set the breeding season to be the anniversary season. Hence, we obtain  $\mathbb{D}_1 = \mathbb{F}_B$  and  $\mathbb{D}_2 = \mathbb{F}_N$ , where  $\mathbb{F}_B$  and  $\mathbb{F}_N$  are as they appear in Sample et al. (2019, p.5).

Migration matrices are defined for each stage in each season. We have altered the migration matrices defined in Sample et al. (2019), such that now there is mortality associated with migration. The migration matrices are the same for all stage and season combinations, and are given by

$$P_1^1 = P_2^1 = P_1^2 = P_2^2 = \begin{bmatrix} 0.6 & 0.4 \\ 0.4 & 0.6 \end{bmatrix}, \quad S_1^1 = S_2^1 = S_1^2 = S_2^2 = \begin{bmatrix} 1 & 0.8 \\ 0.8 & 1 \end{bmatrix} \quad (2.14a)$$

and so

$$M_1^1 = M_2^1 = M_1^2 = M_2^2 = \begin{bmatrix} 0.6 & 0.32 \\ 0.32 & 0.6 \end{bmatrix}.$$

Recall that:  $P_k^i \in \mathbb{R}_+^{n \times n}$  contains the proportion of stage  $i$  individuals that migrate in season  $k$ ;  $S_k^i \in \mathbb{R}_+^{n \times n}$  contains the survival probability of stage  $i$  individuals during migration in season  $k$ ;  $M_k^i \in \mathbb{R}_+^{n \times n}$  contains the probability that an individual in stage  $i$  migrates along a pathway in season  $k$  and survives, see Table 2.2. Mortality associated with migration is captured via the column sums of the  $M_k^i$  all being less than one.

The seasonal matrices are constructed using (2.4) and are given by

$$A_1 = \begin{bmatrix} 0 & 0.3999 & 0 & 0.2133 \\ 0.4800 & 0.5400 & 0.2560 & 0.2880 \\ 0 & 0.1860 & 0 & 0.3488 \\ 0.1920 & 0.2240 & 0.3600 & 0.4200 \end{bmatrix}$$

$$A_2 = \begin{bmatrix} 0.4800 & 0 & 0.2560 & 0 \\ 0 & 0.5400 & 0 & 0.2880 \\ 0.1920 & 0 & 0.3600 & 0 \\ 0 & 0.2240 & 0 & 0.4200 \end{bmatrix}.$$

Further, the seasonal survival matrices are constructed using (2.7) and are given by

$$\hat{A}_1 = \begin{bmatrix} 0 & 0.6650 & 0 & 0.5332 \\ 0.8000 & 0.9000 & 0.6400 & 0.7200 \\ 0 & 0.4650 & 0 & 0.5813 \\ 0.4800 & 0.5600 & 0.6000 & 0.7000 \end{bmatrix}$$

$$\hat{A}_2 = \begin{bmatrix} 0.8000 & 0 & 0.6400 & 0 \\ 0 & 0.9000 & 0 & 0.7200 \\ 0.4800 & 0 & 0.6000 & 0 \\ 0 & 0.5600 & 0 & 0.7000 \end{bmatrix},$$

and, consequently by (2.2), the annual cycle matrix is

$$\mathcal{A} = \begin{bmatrix} 0 & 0.2396 & 0 & 0.1917 \\ 0.3145 & 0.3561 & 0.2419 & 0.2765 \\ 0 & 0.1437 & 0 & 0.1665 \\ 0.1882 & 0.2150 & 0.2085 & 0.2409 \end{bmatrix}.$$

Thus, summing the columns of  $\mathcal{A}$ , the habitat contribution metrics (see (2.13)) are equal to

$$C(\mathcal{P}_0) = \mathbf{1}^T \mathcal{A} = [0.5027 \quad 0.9545 \quad 0.4505 \quad 0.8756]. \quad (2.14b)$$

By inspecting the above vector, we see that individuals that start season 1 in habitat 1 contribute more to the total population than individuals that start in habitat 2. Furthermore, in both habitats, individuals that are adults in season 1 contribute more to the total population than individuals that are juveniles in season 1. Adults that start season 1 in habitat 1 are the population state that contribute the most to the total population. Moreover, we see that over the course of a year none of the population states are replacing themselves (as the habitat contribution metrics are all less than one) and so this population is a sink and is decreasing in the short term. The habitat contribution

metrics are related to the asymptotic growth rate  $\lambda$  via (2.21) and, from this equation, it follows in this case that  $\lambda < 1$ . Thus, the population is declining long term too, as we would expect.

We now specify a pathway in both seasons ( $\phi = 2, \Phi = \{1, 2\}$ ), hence all the distinct migratory routes are

$$P_1 = 1 \rightarrow 1 \rightarrow 1, \quad P_2 = 1 \rightarrow 1 \rightarrow 2, \quad P_3 = 1 \rightarrow 2 \rightarrow 1, \\ P_4 = 1 \rightarrow 2 \rightarrow 2, \\ P_5 = 2 \rightarrow 1 \rightarrow 1, \quad P_6 = 2 \rightarrow 1 \rightarrow 2, \quad P_7 = 2 \rightarrow 2 \rightarrow 1, \\ P_8 = 2 \rightarrow 2 \rightarrow 2. \quad (2.14c)$$

Here:  $P_1$  and  $P_8$  are (the migratory routes of) resident populations;  $P_2$  and  $P_7$  are resident in season 1 and migrate in season 2;  $P_3$  and  $P_6$  migrate in both seasons;  $P_4$  and  $P_5$  migrate in season 1 and are resident in season 2.

For all distinct migratory routes, we calculate subpopulation pathway contribution metrics using (2.11)

$$C(P_1) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,11} \otimes J_2))(\hat{A}_1 \circ (E_{2,11} \otimes J_2))) \\ = [0.7200 \quad 1.3432 \quad 0 \quad 0], \\ C(P_2) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,21} \otimes J_2))(\hat{A}_1 \circ (E_{2,11} \otimes J_2))) \\ = [0.4480 \quad 0.8239 \quad 0 \quad 0], \\ C(P_3) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,12} \otimes J_2))(\hat{A}_1 \circ (E_{2,21} \otimes J_2))) \\ = [0.3456 \quad 0.7008 \quad 0 \quad 0], \\ C(P_4) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,22} \otimes J_2))(\hat{A}_1 \circ (E_{2,21} \otimes J_2))) \\ = [0.3360 \quad 0.6710 \quad 0 \quad 0], \\ C(P_5) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,11} \otimes J_2))(\hat{A}_1 \circ (E_{2,12} \otimes J_2))) \\ = [0 \quad 0 \quad 0.5760 \quad 1.0746], \\ C(P_6) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,21} \otimes J_2))(\hat{A}_1 \circ (E_{2,12} \otimes J_2))) \\ = [0 \quad 0 \quad 0.3584 \quad 0.6591], \\ C(P_7) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,12} \otimes J_2))(\hat{A}_1 \circ (E_{2,22} \otimes J_2))) \\ = [0 \quad 0 \quad 0.4320 \quad 0.8760], \\ C(P_8) = \mathbf{1}^T ((\hat{A}_2 \circ (E_{2,22} \otimes J_2))(\hat{A}_1 \circ (E_{2,22} \otimes J_2))) \\ = [0 \quad 0 \quad 0.4200 \quad 0.8388]. \quad (2.14d)$$

All the distinct migratory routes in (2.14c) have a pathway specified in season 1, resulting in the vectors  $C(P_i)$  only being populated in the sub-vector associated with the initial habitat. The pathway contribution metrics indicate that  $P_1$  and  $P_5$  are the highest quality migratory routes. In fact, the adults in the subpopulations that use these routes are replacing themselves (as the contribution metrics are greater than one), despite all the habitat contribution metrics being less than one. Therefore, managers could increase the total proportion of the population that takes these routes to increase the total population size.

**Example 2.2.** Here we provide a general example to consider an annual cycle model with four seasons and two habitats ( $s = 4, n = 2$ ). Assume that only the second season has a specified pathway (leading to  $\phi = 1$  and  $\Phi = 2$ ) which tracks the subpopulation that travels from habitat 1 to 2. That is,  $\mathcal{P} = 0 \nrightarrow 1 \rightarrow 2 \nrightarrow 0 \nrightarrow 0$ . Using (2.11), the per capita subpopulation pathway contribution metrics are given by

$$C(\mathcal{P}) := \mathbf{1}_{2c}^T (A_4 A_3 (\hat{A}_2 \circ (E_{2,21} \otimes J_c)) A_1) \\ = \mathbf{1}_{cn}^T \left( A_4 A_3 \begin{bmatrix} 0 & 0 \\ (\hat{A}_2)_{21} & 0 \end{bmatrix} A_1 \right).$$

Routine blockwise matrix multiplication gives

$$C(\mathcal{P}) = \text{row} \left[ \left[ \left( \sum_{j=1}^2 \mathbf{1}_c^T ((A_4)_{j1} (A_3)_{12} + (A_4)_{j2} (A_3)_{22}) \right) (\hat{A}_2)_{21} (A_1)_{11} \right] \right]. \quad (2.15)$$

Using (2.12), the per capita metapopulation pathway contribution metrics are given by

$$\begin{aligned} \tilde{\mathbf{C}}(\mathcal{P}) &:= \mathbb{1}_{2c}^T (A_4 I_{2c} A_3 I_{2c} (\hat{A}_2 \circ (E_{2,21} \otimes J_c)) (I_{2c} \otimes (\mathbb{P}_2)_{21}) A_1 I_{2c}) \\ &= \mathbb{1}_{2c}^T \left( A_4 A_3 \begin{bmatrix} 0 & 0 \\ (\hat{A}_2)_{21} & 0 \end{bmatrix} \begin{bmatrix} (\mathbb{P}_2)_{21} & 0 \\ 0 & (\mathbb{P}_2)_{21} \end{bmatrix} A_1 \right). \end{aligned}$$

Similarly

$$\tilde{\mathbf{C}}(\mathcal{P}) = \text{row} \left[ \begin{array}{c} \left( \sum_{j=1}^2 \mathbb{1}_c^T ((A_4)_{j1} (A_3)_{12} + (A_4)_{j2} (A_3)_{22}) \right) (A_2)_{21} (A_1)_{11} \\ \left( \sum_{j=1}^2 \mathbb{1}_c^T ((A_4)_{j1} (A_3)_{12} + (A_4)_{j2} (A_3)_{22}) \right) (A_2)_{21} (A_1)_{12} \end{array} \right]. \quad (2.16)$$

Both (2.15) and (2.16), quantify how much an individual travelling from habitat 1 to habitat 2 in season 2 contributes to the overall population. Notice that the difference between (2.15) and (2.16) is that  $(\hat{A}_2)_{21}$  appears in the former, whilst  $(A_2)_{21}$  appears in the latter. So, in (2.15), only the demography and migratory survival of individuals travelling from habitat 1 to 2 is recorded during season 2. But in (2.16) the proportion of the population that travel from habitat 1 to habitat 2 during season 2 and survive is recorded.

**Example 2.3.** Here, we provide an illustrative example to highlight the subtle distinction between models in which seasons  $k - 1$  and  $k + 1$  each have a specified pathway but season  $k$  does not; and, models in which seasons  $k - 1$ ,  $k$  and  $k + 1$  all have a specified pathway. Still considering a general annual cycle model with four seasons and two habitats ( $s = 4$ ,  $n = 2$ ); we specify two migratory routes denoted by  $\mathcal{P}_1$  and  $\mathcal{P}_2$ .

The first migratory route,  $\mathcal{P}_1$ , specifies pathways in seasons 2 and 4 (leading to  $\phi_1 = 2$  and  $\Phi_1 = \{2, 4\}$ ). In particular, during season 2, the pathway from habitat 1 to habitat 2 is specified; and, in season 4 the pathway from habitat 1 to itself is specified (individuals remain resident in habitat 1 during season 4). So  $\mathcal{P}_1 := 0 \nrightarrow 1 \rightarrow 2 \nrightarrow 1 \rightarrow 1$ .

The second migratory route,  $\mathcal{P}_2$ , specifies pathways in seasons 2, 3 and 4 (leading to  $\phi_2 = 3$  and  $\Phi_2 = \{2, 3, 4\}$ ). In particular, during seasons 2 and 4, the pathways that are specified in  $\mathcal{P}_1$  are specified again; in season 3, the pathway from habitat 2 to habitat 1 is specified. So  $\mathcal{P}_2 := 0 \nrightarrow 1 \rightarrow 2 \rightarrow 1 \rightarrow 1$ . Hence, for  $\mathcal{P}_2$  the proportion of individuals travelling from habitat 2 to habitat 1 during the third season is recorded in the calculation of the pathway contribution metrics, but for  $\mathcal{P}_1$  the proportion of individuals travelling from habitat 2 to habitat 1 during the third season is not recorded.

The pathway contribution metrics are computed by standard block-wise matrix multiplication. For  $\mathcal{P}_1$ ,

$$\begin{aligned} \mathbf{C}(\mathcal{P}_1) &:= \mathbb{1}_{2c}^T ((\hat{A}_4 \circ (E_{2,11} \otimes J_c)) A_3 (\hat{A}_2 \circ (E_{2,21} \otimes J_c)) A_1) \\ &= \mathbb{1}_{2c}^T \left( \begin{bmatrix} (\hat{A}_4)_{11} & 0 \\ 0 & 0 \end{bmatrix} A_3 \begin{bmatrix} 0 & 0 \\ (\hat{A}_2)_{21} & 0 \end{bmatrix} A_1 \right) \\ &= \left[ \mathbb{1}_c^T (\hat{A}_4)_{11} (A_3)_{12} (\hat{A}_2)_{21} (A_1)_{11} \quad \mathbb{1}_c^T (\hat{A}_4)_{11} (A_3)_{12} (\hat{A}_2)_{21} (A_1)_{12} \right], \end{aligned} \quad (2.17)$$

and

$$\begin{aligned} \tilde{\mathbf{C}}(\mathcal{P}_1) &:= \mathbb{1}_{2c}^T ((\hat{A}_4 \circ (E_{2,11} \otimes J_c)) (I_{2c} \otimes (\mathbb{P}_4)_{11}) A_3 I_{2c} (\hat{A}_2 \circ (E_{2,21} \otimes J_c)) \\ &\quad \times (I_{2c} \otimes (\mathbb{P}_2)_{21}) A_1 I_{2c}) \\ &= \mathbb{1}_{2c}^T \left( \begin{bmatrix} (\hat{A}_4)_{11} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} (\mathbb{P}_4)_{11} & 0 \\ 0 & (\mathbb{P}_4)_{11} \end{bmatrix} A_3 \begin{bmatrix} 0 & 0 \\ (\hat{A}_2)_{21} & 0 \end{bmatrix} \right. \\ &\quad \times \left. \begin{bmatrix} (\mathbb{P}_2)_{21} & 0 \\ 0 & (\mathbb{P}_2)_{21} \end{bmatrix} A_1 \right) \\ &= \mathbb{1}_{2c}^T \left[ \begin{array}{cc} (A_4)_{11} (A_3)_{12} (A_2)_{21} (A_1)_{11} & (A_4)_{11} (A_3)_{12} (A_2)_{21} (A_1)_{12} \\ 0 & 0 \end{array} \right] \\ &= \left[ \mathbb{1}_c^T (A_4)_{11} (A_3)_{12} (A_2)_{21} (A_1)_{11} \quad \mathbb{1}_c^T (A_4)_{11} (A_3)_{12} (A_2)_{21} (A_1)_{12} \right]. \end{aligned}$$

For  $\mathcal{P}_2$ ,

$$\begin{aligned} \mathbf{C}(\mathcal{P}_2) &:= \mathbb{1}_{2c}^T ((\hat{A}_4 \circ (E_{2,11} \otimes J_c)) (\hat{A}_3 \circ (E_{2,12} \otimes J_c)) (\hat{A}_2 \circ (E_{2,21} \otimes J_c)) A_1) \\ &= \mathbb{1}_{2c}^T \left( \begin{bmatrix} (\hat{A}_4)_{11} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} 0 & (\hat{A}_3)_{12} \\ 0 & 0 \end{bmatrix} \begin{bmatrix} 0 & 0 \\ (\hat{A}_2)_{21} & 0 \end{bmatrix} A_1 \right) \\ &= \mathbb{1}_{2c}^T \left[ \begin{array}{cc} (\hat{A}_4)_{11} (\hat{A}_3)_{12} (\hat{A}_2)_{21} (A_1)_{11} & (\hat{A}_4)_{11} (\hat{A}_3)_{12} (\hat{A}_2)_{21} (A_1)_{12} \\ 0 & 0 \end{array} \right] \\ &= \left[ \mathbb{1}_c^T (\hat{A}_4)_{11} (\hat{A}_3)_{12} (\hat{A}_2)_{21} (A_1)_{11} \quad \mathbb{1}_c^T (\hat{A}_4)_{11} (\hat{A}_3)_{12} (\hat{A}_2)_{21} (A_1)_{12} \right]. \end{aligned} \quad (2.18)$$

Notice, that  $\mathbf{C}(\mathcal{P}_1) \neq \mathbf{C}(\mathcal{P}_2)$ , as in (2.18) we have  $(\hat{A}_3)_{12}$ , rather than  $(A_3)_{12}$  which appears in (2.17). However,  $\tilde{\mathbf{C}}(\mathcal{P}_1) = \tilde{\mathbf{C}}(\mathcal{P}_2)$ , as the proportion of individuals migrating during season 3 is already included in the calculation of  $\tilde{\mathbf{C}}(\mathcal{P}_i)$ . In other words, since  $\tilde{\mathbf{C}}(\mathcal{P})$  already accounts for the size of the subpopulation travelling along pathways, all elements in the products in (2.10) are blocks of the seasonal matrices  $A_k$ , regardless of whether or not the season has a specified pathway. That is,

$$\begin{aligned} \tilde{\mathbf{C}}(\mathcal{P}_2) &= \tilde{\mathbf{C}}(\mathcal{P}_1) \\ &= \left[ \mathbb{1}_c^T (A_4)_{11} (A_3)_{12} (A_2)_{21} (A_1)_{11} \quad \mathbb{1}_c^T (A_4)_{11} (A_3)_{12} (A_2)_{21} (A_1)_{12} \right]. \end{aligned}$$

### 2.5. Relating habitat and pathway contribution metrics

Here, we take inspiration from Wiederholt et al. (2018) and demonstrate how the habitat contribution metrics  $\mathbf{C}$  may be expressed in terms of a linear combination of pathway contribution metrics. For each combination of seasons that have specified pathways,  $\Phi$ , a number of distinct migratory routes can be specified. Assuming that pathways between all habitats may be taken in every season, the number of distinct migratory routes,  $\gamma$ , for a specified  $\Phi$  is given by

$$\gamma := n^{\phi+a},$$

where  $a$  is the number of entries in  $\Phi$  for which  $\Phi(i) + 1 \notin \Phi$ , owing to the choice of pathway in consecutive seasons relying on each other. Recall that  $\phi$  is the number of seasons for which a pathway is specified. For example, for a model with four seasons, two habitats and  $\Phi = \{1, 3, 4\}$ , we see that  $\phi = 3$  and  $a = 2$ , as 2 and 5 are not in  $\Phi$ . Therefore, there are  $\gamma = 2^5 = 32$  distinct migratory routes.

For  $i \in \{1, \dots, \gamma\}$  let  $\mathcal{P}_i$  store the  $i$ th distinct migratory route. Then, for each distinct migratory route,  $\tilde{\mathbf{C}}(\mathcal{P}_i)$  corresponds to a distinct subpopulation and the habitat contribution metrics,  $\mathbf{C}$ , correspond to the total population; therefore,  $\mathbf{C}$  is given by

$$\mathbf{C} = \sum_{i=1}^{\gamma} \tilde{\mathbf{C}}(\mathcal{P}_i). \quad (2.19)$$

That is, summing the contributions of individuals from each distinct subpopulation gives the per capita contributions structured by the initial habitat. For example, the contribution of an individual that starts the annual cycle in stage 1 and habitat 1,  $C_1^1$ , can be obtained by summing the  $\tilde{C}_1^1(\mathcal{P}_i)$  metrics across all possible migratory routes. The habitat contribution metrics are equal to the sum of all possible metapopulation pathway contribution metrics. Consequently, the metapopulation pathway contribution metrics provide another layer of granularity compared to habitat contribution metrics, and can thus highlight the importance of a given migratory route.

We comment that, in reality, migrants may not use all pathways in every season; hence, not all distinct migratory routes  $\mathcal{P}_i$  are biologically valid. However, if  $\mathcal{P}_i$  is not a valid migratory route,  $\tilde{\mathbf{C}}(\mathcal{P}_i)$  will be zero. Thus, (2.19) is still true. For complex models, using all distinct migratory routes (including invalid migratory routes) results in large  $\gamma$ . In this situation, only the contribution metrics corresponding to the distinct migratory routes that are biologically valid need to be calculated for use in (2.19).

In special cases, a linear combination of the  $C(\mathcal{P}_i)$  metrics can be used to derive  $\mathbf{C}$ . We define  $\hat{\mathbb{P}}_i \in \mathbb{R}^{cn \times cn}$  by

$$\hat{\mathbb{P}}_i := \prod_{\tau=1}^{\phi} I_n \otimes (\mathbb{P}_{\phi(\tau)} \mathcal{P}_i \mathcal{P}_{i(\phi(\tau)+1)} \mathcal{P}_i \mathcal{P}_{i(\phi(\tau))}).$$

That is, along the diagonal,  $\hat{\mathbb{P}}_i$  stores the proportion of individuals that migrate along  $\mathcal{P}_i$ . Notice that

$$\hat{\mathbb{P}}_i = \prod_{\tau=1}^{\phi} \mathbf{P}_{\phi(\tau)} = \prod_{k=1}^s \mathbf{P}_k.$$

Then, when either only the first season has a specified pathway, or when  $\mathcal{P}_k^i$  is the same for all  $i \in \{1, \dots, c\}$ , we have that  $\hat{\mathbb{P}}_i = \alpha I_{cn}$ , where  $\alpha \in \mathbb{R}_+$ . In particular, the habitat contribution metrics,  $\mathbf{C}$ , are given by

$$\mathbf{C} = \sum_{i=1}^{\gamma} C(\mathcal{P}_i) \hat{\mathbb{P}}_i, \tag{2.20}$$

where  $C(\mathcal{P}_i)$  is defined as in (2.11). Hence, (2.20) is a multi-state version of Wiederholt et al. (2018, Eq. (5)).

We now provide an illustrative example where the pathway contribution metrics may be obtained from  $C(\mathcal{P}_i)$ .

**Example 2.4.** Here we use the same model as in Example 2.1 and show that the habitat contribution metrics can be recovered from the pathway contribution metrics.

The migration matrices containing the migratory proportions are the same for all season and stage combinations, see (2.14a). Therefore, for every distinct migratory route  $\mathcal{P}_i$ , we know that  $\hat{\mathbb{P}}_i = \alpha I_{cn}$ . In particular: for  $\mathcal{P}_1$  and  $\mathcal{P}_8$ ,  $\hat{\mathbb{P}}_i = 0.36 I_4$ ; for  $\mathcal{P}_2, \mathcal{P}_4, \mathcal{P}_5$  and  $\mathcal{P}_7$ ,  $\hat{\mathbb{P}}_i = 0.24 I_4$ ; for  $\mathcal{P}_3$  and  $\mathcal{P}_6$ ,  $\hat{\mathbb{P}}_i = 0.16 I_4$ . Hence, we input the subpopulation pathway metrics for all distinct migratory routes (see (2.14d)) into (2.20) and obtain

$$\mathbf{C} = [0.5027 \quad 0.9545 \quad 0.4505 \quad 0.8756].$$

The above vector is equal to that in (2.14b); thus, the habitat contribution metrics have been recovered.

### 2.6. Relating contribution metrics to asymptotic growth

The contribution metrics developed in Runge et al. (2006) and Wiederholt et al. (2018) (and the habitat contribution metrics in Sample et al. (2019)) can all be related to the asymptotic growth rate of the population. Here, we show that summing over the metapopulation pathway contribution metrics weighted by the stable stage structure of the population gives the asymptotic growth rate of the population.

Let  $\lambda$  be the dominant eigenvalue of  $\mathcal{A}$  and  $\mathbf{w}$  be the corresponding right eigenvector, scaled such that the entries of  $\mathbf{w}$  are nonnegative and sum to one. In other words,  $\mathbf{w}$  is the standardised stable stage-structure of the annual cycle population model. In the case that  $\mathcal{A}$  is irreducible, the eigenvalue  $\lambda$  is a simple eigenvalue of  $\mathcal{A}$  by the Perron–Frobenius Theorem, and so the above conditions determine  $\mathbf{w}$  uniquely.

Hence,  $\mathcal{A}\mathbf{w} = \lambda\mathbf{w}$ , and so

$$\mathbf{C}\mathbf{w} := \mathbb{1}_{cn}^T \mathcal{A}\mathbf{w} = \mathbb{1}_{cn}^T \lambda\mathbf{w} = \lambda \|\mathbf{w}\|_1 = \lambda. \tag{2.21}$$

Substituting (2.19) for  $\mathbf{C}$ , gives

$$\left( \sum_{i=1}^{\gamma} \tilde{C}(\mathcal{P}_i) \right) \mathbf{w} = \sum_j \left( \sum_{i=1}^{\gamma} \tilde{C}(\mathcal{P}_i) \right) \mathbf{w}_j = \lambda. \tag{2.22}$$

Thus, the sum of the metapopulation pathway contribution metrics,  $\tilde{C}(\mathcal{P})$ , weighted by the stable stage structure, equals the overall asymptotic growth rate of the total population. Recall that  $\tilde{C}(\mathcal{P}_i)$  contains the per capita contribution, for each initial population state, of the (distinct) subpopulation that travels along the (distinct) migratory route  $\mathcal{P}_i$  during the annual cycle. Furthermore, the summation of the metapopulation pathway contribution metrics for all distinct subpopulations

gives the per capita contribution of each initial state of the total population. Recall that the state contribution metrics  $C_j^i$  (the entries in  $\mathbf{C}$ ) can be thought of as the number of individuals (across the total population) that are generated over an annual cycle by an individual that is initially in stage  $i$  and habitat  $j$ . Hence, it is intuitive that the average of the state contribution metrics weighted by the stable stage distribution is the total population generated in the next annual time step, and in this particular case equals the asymptotic growth rate of the population.

Furthermore, in the special cases where (2.20) holds, we have

$$\left( \sum_{i=1}^{\gamma} C(\mathcal{P}_i) \hat{\mathbb{P}}_i \right) \mathbf{w} = \sum_j \left( \sum_{i=1}^{\gamma} C(\mathcal{P}_i) \hat{\mathbb{P}}_i \right) \mathbf{w}_j = \lambda. \tag{2.23}$$

Again, the above equality is intuitive once we know that the  $C(\mathcal{P}_i)$  metrics can be used to calculate  $\mathbf{C}$ .

Eq. (2.22) (or (2.23)) can be used to provide insight into the trade-offs between asymptotic and transient dynamics, captured presently by  $\tilde{C}(\mathcal{P}_i)$  (or  $C(\mathcal{P}_i)$ ) and  $\lambda$ , respectively. For example, if a particular contribution metric increases by some change or perturbation to  $\mathcal{A}$ ; then, for a fixed  $\lambda$ , the corresponding component of  $\mathbf{w}$  must decrease, all else remaining the same, in order to maintain equality in (2.22) (or (2.23)).

### 2.7. Averaging contribution metrics

Here we provide easy to compute matrix formulae to calculate the average contribution to the total population of an initial habitat or stage for a subpopulation that follows a particular migratory route. The first metric we define averages the metapopulation pathway contribution metrics  $\tilde{C}(\mathcal{P})$  over stage, to assess the quality of a habitat, regardless of stage. The second metric we define averages  $\tilde{C}(\mathcal{P})$  over habitat, to assess the contribution of an initial stage.

#### 2.7.1. Averaging over stage

The contribution metrics stored in  $\tilde{C}(\mathcal{P})$  can be averaged over stage to assess the quality of habitats. There is an averaged contribution metric associated with each habitat  $j \in \{1, \dots, n\}$ , denoted by  $\tilde{C}_j(\mathcal{P})$ . Each  $\tilde{C}_j(\mathcal{P})$  is the average contribution of an individual that starts the annual cycle in habitat  $j$  and migrates along  $\mathcal{P}$ . The calculation of  $\tilde{C}_j(\mathcal{P})$  requires knowledge of the population structure at the start of the annual cycle,  $\mathbf{x}$ . We provide a matrix formulation that simultaneously calculates all  $\tilde{C}_j(\mathcal{P})$  metrics, given by

$$\begin{aligned} \tilde{\mathbf{H}}(\mathcal{P}) &:= \left( \sum_{j=1}^n E_{n,jj} \otimes \mathbb{1}_c^T \right) \left( (\mathbf{x} \circ \tilde{C}(\mathcal{P}))^T \oslash \left( \left( \sum_{j=1}^n E_{n,jj} \otimes J_c \right) \mathbf{x} \right) \right) \\ &= \begin{bmatrix} \mathbb{1}_c^T & & \\ & \ddots & \\ & & \mathbb{1}_c^T \end{bmatrix} \left( (\mathbf{x} \circ \tilde{C}(\mathcal{P}))^T \oslash \begin{bmatrix} J_c & & \\ & \ddots & \\ & & J_c \end{bmatrix} \mathbf{x} \right) \\ &=: \begin{bmatrix} \tilde{C}_1(\mathcal{P}) \\ \vdots \\ \tilde{C}_n(\mathcal{P}) \end{bmatrix} \in \mathbb{R}_+^n. \end{aligned} \tag{2.24}$$

The mathematical notation is detailed in Section 2.1, and recall that  $\oslash$  denotes Hadamard division. The definition of  $\oslash$  means that the averaged contribution of an empty habitat is zero. The vector  $\tilde{\mathbf{H}}(\mathcal{P})$  is structured by the habitat in which a subpopulation starts the annual cycle. For clarity, note that  $\tilde{\mathbf{H}}(\mathcal{P})$  is a column vector, whilst the pathway contribution metrics presented so far are row vectors.

We have chosen to present our formula using vectors and matrices to encode more information in one calculation that is easy to implement numerically. However, setting  $x_j = \mathbb{1}_c^T \mathbf{x}_j$ , which is the number of individuals in habitat  $j$  at the start of the annual cycle, routine calculations starting from (2.24) show that

$$\tilde{C}_j(\mathcal{P}) = \sum_{i=1}^c \frac{x_j^i \tilde{C}_j^i(\mathcal{P})}{x_j}, \tag{2.25}$$



whenever  $x_j$  is nonzero. Hence, each block of our formula computes (Sample et al., 2019, Eq. (9)) for a different initial habitat. We provide a derivation of the above calculation in Appendix C.1.

The size of  $\tilde{C}_j$  indicates whether habitat  $j$  is a source or a sink for the focal subpopulation. If  $\tilde{C}_j(\mathcal{P}) > 1$ , then habitat  $j$  is said to be a source for the subpopulation that follows the migratory route defined by  $\mathcal{P}$ . Alternatively, if  $\tilde{C}_j(\mathcal{P}) < 1$ , then habitat  $j$  is said to be a sink for the subpopulation that follows the migratory route defined by  $\mathcal{P}$ .

We note that the averaged contribution metrics depend on the initial population structure, here denoted  $\mathbf{x}$ , and not just the annual cycle matrix. Thus, the year that the population is measured will influence the value of the averaged contribution metrics.

### 2.7.2. Averaging over habitat

Similarly, the contribution metrics stored in  $\tilde{\mathbf{C}}(\mathcal{P})$  can be averaged over habitat to assess the contribution of stages. There is an averaged contribution metric associated with each stage  $i \in \{1, \dots, c\}$ , denoted by  $\tilde{C}^i(\mathcal{P})$ . Each  $\tilde{C}^i(\mathcal{P})$  is the average contribution of an individual that starts the annual cycle in stage  $i$  and migrates along  $\mathcal{P}$ . The calculation of  $\tilde{C}^i(\mathcal{P})$  requires knowledge of the population structure at the start of the annual cycle,  $\mathbf{x}$ . We provide a matrix formulation that simultaneously calculates all  $\tilde{C}^i(\mathcal{P})$  metrics, given by

$$\begin{aligned} \tilde{\mathbf{S}}(\mathcal{P}) &:= \left( \sum_{i=1}^c \mathbb{1}_n^T \otimes E_{c,ii} \right) \left( (\mathbf{x} \circ \tilde{\mathbf{C}}(\mathcal{P})^T) \otimes \left( \left( \sum_{i=1}^c J_n \otimes E_{c,ii} \right) \mathbf{x} \right) \right) \\ &= [I_c \quad \dots \quad I_c] \left( \mathbf{x} \circ \tilde{\mathbf{C}}(\mathcal{P})^T \otimes \begin{bmatrix} I_c & \dots & I_c \\ \vdots & & \vdots \\ I_c & \dots & I_c \end{bmatrix} \mathbf{x} \right) =: \begin{bmatrix} \tilde{C}^1(\mathcal{P}) \\ \vdots \\ \tilde{C}^c(\mathcal{P}) \end{bmatrix}. \end{aligned} \quad (2.26)$$

Recall from Section 2.1 that  $I_c$  denotes the  $c \times c$  identity matrix.

It can be shown by a simplification of (2.26) (see Appendix C.2) that

$$\tilde{C}^i(\mathcal{P}) = \sum_{j=1}^n \frac{x_j^i \tilde{C}_j^i}{x^i}, \quad (2.27)$$

whenever  $x^i$  is nonzero. Here,  $x^i = \sum_{j=1}^n x_j^i$  is the total number of individuals in stage  $i$  at the start of the annual cycle. Since  $\tilde{C}_j^i$  contains information about the proportion of individuals migrating, each block of our formula computes (Sample et al., 2019, Eq. (12)) for a different starting stage. Thus, each  $\tilde{C}^i(\mathcal{P})$  is the per capita contribution of the subpopulation that travels the migratory route defined by  $\mathcal{P}$  and starts the annual cycle in stage  $i$ .

Again, we note that these averaged contribution metrics depend on the initial population structure, not just the annual cycle matrix. The effect of the population structure  $\mathbf{x}$  on  $\tilde{\mathbf{H}}(\mathcal{P})$  and  $\tilde{\mathbf{S}}(\mathcal{P})$  will be explored further in Smith (2023).

## 3. Case studies

Here, we calculate our contribution metrics for a range of annual cycle models. First, we demonstrate how our framework generalises that in Wiederholt et al. (2018), by extending their scalar population model into a matrix population model. Next, we use an annual cycle model for a North American migratory monarch butterfly population with multiple stages, habitats and seasons to explore the range of contribution metrics that can be calculated using our framework. These metrics include full migratory routes, which previous frameworks could not capture. Finally, we provide an example that details how contribution metrics can be used to design a simple optimal single time-step control solution for the conservation of a population.

**Example 3.1.** We illustrate the connection between our subpopulation pathway contribution metric and the one defined in Wiederholt et al. (2018), which considers annual cycle models with two seasons and two stages (representing juvenile and adult individuals). Borrowing the

notation of Wiederholt et al. (2018), habitats are defined to be either the origin  $o$ , intermediate  $i$ , or destination  $d$ ; the population travels from  $o$  to  $i$  during season 1, and from  $i$  to  $d$  during season 2.

The adult survival probability,  $A^{oid}$ , and per capita juvenile recruitment,  $J^{oid}$ , for a focal migratory route during the annual cycle where the breeding season is the anniversary season, are given by

$$A^{oid} = (s_{oi,B}^a \cdot s_{i,B}^a) \cdot (s_{id,N}^a \cdot s_{d,N}^a) \quad \text{and} \quad J^{oid} = (s_{oi,B}^a \cdot s_{i,B}^a \cdot r_{i,B}) \cdot (s_{id,N}^j \cdot s_{d,N}^j), \quad (3.1)$$

where: superscripts  $a$  and  $j$  refer to the adult and juvenile stages, respectively; subscripts  $B$  and  $N$  refer to the breeding and non-breeding seasons, respectively; brackets indicate the split of seasons. Note that Wiederholt et al. use  $s_{j,l,k}^i$  to represent an individual in stage  $i$  migrating from habitat  $j$  to habitat  $l$  in season  $k$ . We have adjusted equations (1) and (2) in Wiederholt et al. (2018) so that in (3.1) migration happens first. For further information see Appendix D. Then, the per capita contribution of a pathway,  $C^{oid}$  is defined to be

$$C^{oid} := A^{oid} + J^{oid} = s_{oi,B}^a s_{i,B}^a s_{id,N}^a s_{d,N}^a + s_{oi,B}^a s_{i,B}^a r_{i,B} s_{id,N}^j s_{d,N}^j. \quad (3.2)$$

Now, we translate the notation of Wiederholt et al. (2018) into our notation. Hence, we consider a model with two seasons, two stages and three habitats ( $s = 2, c = 2, n = 3$ ). We set the breeding and non-breeding seasons to be season 1 and season 2, respectively. Juveniles and adults are set to be stage 1 and stage 2, respectively. For the ease of comparison, we keep the habitat labels  $o, i$  and  $d$ . Both seasons have a specified pathway, hence  $\phi = 2$  and  $\Phi = \{1, 2\}$ . We specify the migratory route to be  $\mathcal{P} := o \rightarrow i \rightarrow d$ .

The demographic matrices associated with habitats  $o, i$  and  $d$ , in season 1 (breeding) and season 2 (non-breeding), are

$$\begin{aligned} D_{o,1} &:= \begin{bmatrix} 0 & s_{o,1}^2 r_{o,1} \\ s_{o,1}^1 & s_{o,1}^2 \end{bmatrix} & D_{o,2} &:= \begin{bmatrix} s_{o,2}^1 & 0 \\ 0 & s_{o,2}^2 \end{bmatrix}, \\ D_{i,1} &:= \begin{bmatrix} 0 & s_{i,1}^2 r_{i,1} \\ s_{i,1}^1 & s_{i,1}^2 \end{bmatrix} & D_{i,2} &:= \begin{bmatrix} s_{i,2}^1 & 0 \\ 0 & s_{i,2}^2 \end{bmatrix}, \\ D_{d,1} &:= \begin{bmatrix} 0 & s_{d,1}^2 r_{d,1} \\ s_{d,1}^1 & s_{d,1}^2 \end{bmatrix} & D_{d,2} &:= \begin{bmatrix} s_{d,2}^1 & 0 \\ 0 & s_{d,2}^2 \end{bmatrix}. \end{aligned}$$

Therefore, from (2.3) we obtain

$$\mathbb{D}_1 = \begin{bmatrix} 0 & s_{o,1}^2 r_{o,1} & 0 & 0 & 0 & 0 \\ s_{o,1}^1 & s_{o,1}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{i,1}^2 r_{i,1} & 0 & 0 \\ 0 & 0 & s_{i,1}^1 & s_{i,1}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{d,1}^2 r_{d,1} \\ 0 & 0 & 0 & 0 & s_{d,1}^1 & s_{d,1}^2 \end{bmatrix} \quad \text{and}$$

$$\mathbb{D}_2 = \begin{bmatrix} s_{o,2}^1 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{o,2}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{i,2}^1 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{i,2}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{d,2}^1 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{d,2}^2 \end{bmatrix}.$$

Furthermore, the matrices storing the probability of surviving migration,  $S_k^i$ , for stage 1 (juveniles) and stage 2 (adults), are

$$S_1^1 := \begin{bmatrix} s_{oo,1}^1 & s_{oi,1}^1 & s_{od,1}^1 \\ s_{io,1}^1 & s_{ii,1}^1 & s_{id,1}^1 \\ s_{do,1}^1 & s_{di,1}^1 & s_{dd,1}^1 \end{bmatrix} \quad S_2^1 := \begin{bmatrix} s_{oo,2}^1 & s_{oi,2}^1 & s_{od,2}^1 \\ s_{io,2}^1 & s_{ii,2}^1 & s_{id,2}^1 \\ s_{do,2}^1 & s_{di,2}^1 & s_{dd,2}^1 \end{bmatrix},$$

$$S_1^2 := \begin{bmatrix} s_{oo,1}^2 & s_{oi,1}^2 & s_{od,1}^2 \\ s_{io,1}^2 & s_{ii,1}^2 & s_{id,1}^2 \\ s_{do,1}^2 & s_{di,1}^2 & s_{dd,1}^2 \end{bmatrix} \quad S_2^2 := \begin{bmatrix} s_{oo,2}^2 & s_{oi,2}^2 & s_{od,2}^2 \\ s_{io,2}^2 & s_{ii,2}^2 & s_{id,2}^2 \\ s_{do,2}^2 & s_{di,2}^2 & s_{dd,2}^2 \end{bmatrix}.$$

Substituting into Eq. (2.5) gives

$$S_1 = \begin{bmatrix} s_{oo,1}^1 & 0 & s_{oi,1}^1 & 0 & s_{od,1}^1 & 0 \\ 0 & s_{oo,1}^2 & 0 & s_{oi,1}^2 & 0 & s_{od,1}^2 \\ s_{io,1}^1 & 0 & s_{ii,1}^1 & 0 & s_{id,1}^1 & 0 \\ 0 & s_{io,1}^2 & 0 & s_{ii,1}^2 & 0 & s_{id,1}^2 \\ s_{do,1}^1 & 0 & s_{di,1}^1 & 0 & s_{dd,1}^1 & 0 \\ 0 & s_{do,1}^2 & 0 & s_{di,1}^2 & 0 & s_{dd,1}^2 \end{bmatrix} \quad \text{and} \quad S_2 = \begin{bmatrix} s_{oo,2}^1 & 0 & s_{oi,2}^1 & 0 & s_{od,2}^1 & 0 \\ 0 & s_{oo,2}^2 & 0 & s_{oi,2}^2 & 0 & s_{od,2}^2 \\ s_{io,2}^1 & 0 & s_{ii,2}^1 & 0 & s_{id,2}^1 & 0 \\ 0 & s_{io,2}^2 & 0 & s_{ii,2}^2 & 0 & s_{id,2}^2 \\ s_{do,2}^1 & 0 & s_{di,2}^1 & 0 & s_{dd,2}^1 & 0 \\ 0 & s_{do,2}^2 & 0 & s_{di,2}^2 & 0 & s_{dd,2}^2 \end{bmatrix}.$$

Recall that, in our notation,  $s_{jl,k}^i$  is the probability that an individual in stage  $i$  survives travelling from habitat  $l$  to habitat  $j$ , during season  $k$ .

The seasonal survival matrices, where migration happens first,  $\hat{A}_k := \mathbb{D}_k S_k$  (see (2.7)), are

$$\hat{A}_1 = \begin{bmatrix} 0 & s_{o,1}^2 r_{o,1} s_{oo,1}^2 & 0 & s_{o,1}^2 r_{o,1} s_{oi,1}^2 & 0 & s_{o,1}^2 r_{o,1} s_{od,1}^2 \\ s_{o,1}^1 s_{oo,1}^1 & s_{o,1}^2 s_{oo,1}^2 & s_{o,1}^1 s_{oi,1}^1 & s_{o,1}^2 s_{oi,1}^2 & s_{o,1}^1 s_{od,1}^1 & s_{o,1}^2 s_{od,1}^2 \\ 0 & s_{i,1}^2 r_{i,1} s_{io,1}^2 & 0 & s_{i,1}^2 r_{i,1} s_{ii,1}^2 & 0 & s_{i,1}^2 r_{i,1} s_{id,1}^2 \\ s_{i,1}^1 s_{io,1}^1 & s_{i,1}^2 s_{io,1}^2 & s_{i,1}^1 s_{ii,1}^1 & s_{i,1}^2 s_{ii,1}^2 & s_{i,1}^1 s_{id,1}^1 & s_{i,1}^2 s_{id,1}^2 \\ 0 & s_{d,1}^2 r_{d,1} s_{do,1}^2 & 0 & s_{d,1}^2 r_{d,1} s_{di,1}^2 & 0 & s_{d,1}^2 r_{d,1} s_{dd,1}^2 \\ s_{d,1}^1 s_{do,1}^1 & s_{d,1}^2 s_{do,1}^2 & s_{d,1}^1 s_{di,1}^1 & s_{d,1}^2 s_{di,1}^2 & s_{d,1}^1 s_{dd,1}^1 & s_{d,1}^2 s_{dd,1}^2 \end{bmatrix},$$

$$\hat{A}_2 = \begin{bmatrix} s_{o,2}^1 s_{oo,2}^1 & 0 & s_{o,2}^1 s_{oi,2}^1 & 0 & s_{o,2}^1 s_{od,2}^1 & 0 \\ 0 & s_{o,2}^2 s_{oo,2}^2 & 0 & s_{o,2}^2 s_{oi,2}^2 & 0 & s_{o,2}^2 s_{od,2}^2 \\ s_{i,2}^1 s_{io,2}^1 & 0 & s_{i,2}^1 s_{ii,2}^1 & 0 & s_{i,2}^1 s_{id,2}^1 & 0 \\ 0 & s_{i,2}^2 s_{io,2}^2 & 0 & s_{i,2}^2 s_{ii,2}^2 & 0 & s_{i,2}^2 s_{id,2}^2 \\ s_{d,2}^1 s_{do,2}^1 & 0 & s_{d,2}^1 s_{di,2}^1 & 0 & s_{d,2}^1 s_{dd,2}^1 & 0 \\ 0 & s_{d,2}^2 s_{do,2}^2 & 0 & s_{d,2}^2 s_{di,2}^2 & 0 & s_{d,2}^2 s_{dd,2}^2 \end{bmatrix}.$$

Then, by (2.11), the subpopulation pathway contribution metric,  $C(P)$ , where the breeding season is the anniversary season, is given by

$$C(P) := \mathbb{1}^T ((\hat{A}_2 \circ (E_{3,di} \otimes J_2)) (\hat{A}_1 \circ (E_{3,io} \otimes J_2)))$$

$$= \begin{bmatrix} 1 & 1 & 1 & 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{d,2}^1 s_{di,2}^1 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{d,2}^2 s_{di,2}^2 & 0 & 0 \end{bmatrix}$$

$$\times \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{i,1}^2 r_{i,1} s_{io,1}^2 & 0 & 0 & 0 & 0 \\ s_{i,1}^1 s_{io,1}^1 & s_{i,1}^2 s_{io,1}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$= \begin{bmatrix} 0 & 0 & s_{d,2}^1 s_{di,2}^1 & s_{d,2}^2 s_{di,2}^2 & 0 & 0 \end{bmatrix}$$

$$\times \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{i,1}^2 r_{i,1} s_{io,1}^2 & 0 & 0 & 0 & 0 \\ s_{i,1}^1 s_{io,1}^1 & s_{i,1}^2 s_{io,1}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

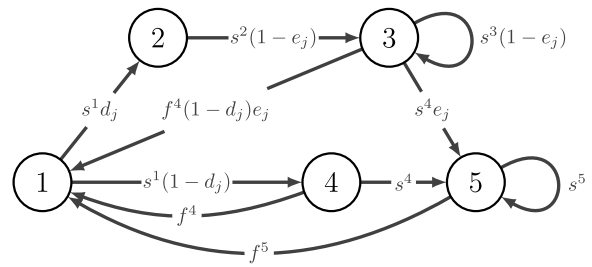


Fig. 3.1. Life cycle graph for monarch butterflies in region  $j \in \{1, 2, 3, 4\}$ . This figure is inspired by Flockhart et al. (2015, Fig. 1).

$$= \begin{bmatrix} s_{d,2}^2 s_{di,2}^2 s_{i,1}^1 s_{io,1}^1 & s_{d,2}^1 s_{di,2}^1 s_{i,1}^2 r_{i,1} s_{io,1}^2 + s_{d,2}^2 s_{di,2}^2 s_{i,1}^1 s_{io,1}^1 & 0 & 0 & 0 & 0 \end{bmatrix}.$$

To more readily compare the above equation to (3.2), we reset the labels above for season 1 and season 2 to  $B$  and  $N$ , respectively. We also reset the labels for stage 1 and stage 2 to  $j$  and  $a$ , respectively. Hence,

$$C(P) = \begin{bmatrix} s_{d,N}^a s_{di,N}^a s_{i,B}^j s_{io,B}^j & s_{d,N}^j s_{di,N}^j s_{i,B}^a r_{i,B} s_{io,B}^a + s_{d,N}^a s_{di,N}^a s_{i,B}^j s_{io,B}^j & 0 & 0 & 0 & 0 \end{bmatrix}.$$

Accounting for the difference between  $s_{jl,k}^i$  in our notation and that in Wiederholt et al. (2018), we see that the second entry equals  $C^{oid}$ . The first entry calculates the contribution of juveniles that transition into adults over the annual cycle. The final four entries are zero as the migratory route  $\mathcal{P}$  has a specified pathway during the first season; all individuals in the focal subpopulation start the annual cycle in habitat  $o$ , and so the contribution of habitats  $i$  and  $d$  is zero. Thus, our subpopulation pathway contribution metric generalises that developed in Wiederholt et al. (2018).

**Example 3.2.** We consider a population model for the monarch butterfly (*Danaus plexippus*) in eastern North America. The population size of migratory monarch butterflies in eastern North America is estimated to have declined from 300–900 million in the 1990s to 33–200 million in recent years (Vidal and Rendón-Salinas, 2014); leading to the eastern monarch migration being classified as an endangered phenomenon (Advani, 2015; Brower et al., 2012). A number of studies have assessed the population viability of the monarch butterfly, including (Advani, 2015; Flockhart et al., 2015). Calculation of the contribution metrics associated with the monarch butterfly population in eastern North America can provide further insight into how best to conserve this iconic species.

We use a model inspired by those in Flockhart et al. (2015) and Sample et al. (2018). Our model is for the female population and contains five stages ( $c = 5$ ), four habitats ( $n = 4$ ) and twelve seasons ( $s = 12$ ). The life stages are: immature individuals, including eggs, larval and pupal development until eclosion (1); eclosed butterflies in their first month of life and in reproductive diapause (2); eclosed butterflies in their second month of life or older and in reproductive diapause (3); eclosed butterflies in their first month of life and in breeding condition (4); and, eclosed butterflies in their second month of life or older and in breeding condition (5). Monarch butterflies complete a long-distance migration over one year between: Mexico (M), Southern US (S), Central US (C) and Northern US (N). Fig. 3.1 depicts the life cycle of female monarch butterflies in region  $j \in \{M, S, C, N\}$ , where nodes represent stages and edges represent transitions between stages. The data used to calculate the demographic rates we use are recorded in the tables in Appendix E.1.

Mexico is a wintering region, whilst the other three regions are breeding regions. The survival rates of migration are given in Fig. 3.2. For each season, Fig. 3.3 depicts the proportion of the population travelling along each pathway. The corresponding matrices  $S_k^i$  and  $P_k^i$  are recorded in Appendix E.2; recall that these matrices are used to

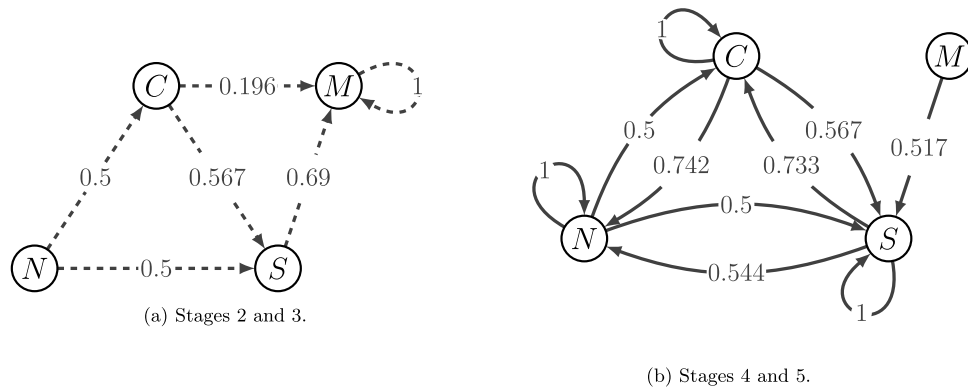


Fig. 3.2. Survival rates along migratory pathways.

Table 3.1  
Pathway contribution metrics for the monarch butterfly annual cycle model considered in Example 3.2.

$\Phi$	Pathway	Subpopulation pathway contribution metrics				Metapopulation pathway contribution metrics					
		$C(\mathcal{P}_i)$				$\tilde{C}(\mathcal{P}_i)$					
1	1 → 1	0	9.62	9.62	0	0	0	9.62	9.62	0	0
2	1 → 1	0	9.62	9.62	0	0	0	9.62	9.62	0	0
3	1 → 1	0	9.62	9.62	0	0	0	9.62	9.62	0	0
4	1 → 2	0	9.62	9.62	0	0	0	9.62	9.62	0	0
5	2 → 2	0	9.25	9.25	0	0	0	9.24	9.24	0	0
	2 → 3	0	1.01	1.01	0	0	0	$3.84 \times 10^{-1}$	$3.84 \times 10^{-1}$	0	0
6	2 → 3	0	13.1	13.1	0	0	0	7.27	7.27	0	0
	2 → 4	0	4.44	4.44	0	0	0	1.97	1.97	0	0
	3 → 3	0	$3.88 \times 10^{-1}$	$3.88 \times 10^{-1}$	0	0	0	$3.82 \times 10^{-1}$	$3.82 \times 10^{-1}$	0	0
	3 → 4	0	$4.29 \times 10^{-3}$	$4.29 \times 10^{-3}$	0	0	0	$2.01 \times 10^{-3}$	$2.01 \times 10^{-3}$	0	0
7	3 → 3	0	7.68	7.68	0	0	0	7.10	7.10	0	0
	3 → 4	0	$9.54 \times 10^{-1}$	$9.54 \times 10^{-1}$	0	0	0	$5.48 \times 10^{-1}$	$5.48 \times 10^{-1}$	0	0
	4 → 3	0	$1.82 \times 10^{-1}$	$1.82 \times 10^{-1}$	0	0	0	$3.35 \times 10^{-2}$	$3.35 \times 10^{-2}$	0	0
	4 → 4	0	2.02	2.02	0	0	0	1.94	1.94	0	0
8	3 → 3	0	9.40	9.40	0	0	0	6.72	6.72	0	0
	3 → 4	0	1.40	1.40	0	0	0	$4.20 \times 10^{-1}$	$4.20 \times 10^{-1}$	0	0
	4 → 3	0	2.69	2.69	0	0	0	$7.46 \times 10^{-1}$	$7.46 \times 10^{-1}$	0	0
	4 → 4	0	2.05	2.05	0	0	0	1.74	1.74	0	0
9	3 → 2	0	3.70	3.70	0	0	0	2.04	2.04	0	0
	3 → 3	0	5.43	5.43	0	0	0	5.43	5.43	0	0
	4 → 2	0	3.71	3.71	0	0	0	2.15	2.15	0	0
	4 → 3	0	$1.55 \times 10^{-2}$	$1.55 \times 10^{-2}$	0	0	0	$6.49 \times 10^{-3}$	$6.49 \times 10^{-3}$	0	0
10	2 → 2	0	4.19	4.19	0	0	0	4.19	4.19	0	0
	3 → 1	0	3.51	3.51	0	0	0	1.58	1.58	0	0
	3 → 2	0	7.01	7.01	0	0	0	3.85	3.85	0	0
11	1 → 1	0	1.58	1.58	0	0	0	1.58	1.58	0	0
	2 → 1	0	8.04	8.04	0	0	0	8.04	8.04	0	0
12	1 → 1	0	9.62	9.62	0	0	0	9.62	9.62	0	0

construct  $\mathbb{S}$  and  $\mathbb{P}$  which are used to calculate the  $\mathbb{M}$  matrices via (2.6).

We take  $\phi = 1$  and set  $\Phi$  to be each season in turn. Since all the population starts the annual cycle in Mexico, only the first block of  $C(\mathcal{P}_i)$  and  $\tilde{C}(\mathcal{P}_i)$  are populated, hence we only record these values in Table 3.1. When the  $\tilde{C}(\mathcal{P}_i)$  metrics are averaged over stage, only  $\tilde{C}_M(\mathcal{P}_i)$  is nonzero and is equal to the nonzero values in the corresponding  $\tilde{C}(\mathcal{P}_i)$ . Similarly, when averaging over stage, only  $\tilde{C}^2(\mathcal{P}_i)$  and  $\tilde{C}^3(\mathcal{P}_i)$  are nonzero and are both equal to the nonzero values in the corresponding  $\tilde{C}(\mathcal{P}_i)$ .

Based on the contribution metrics, the pathway between the South (S) and Central (C) regions in June (season 6) contributes the most. The pathway between Central (C) and North (N) in June contributes the least. Therefore, to increase the total population size, the quality of the route between C and N could be improved. Alternatively, managers could increase the proportion of monarch butterflies that travel between S and C in June. Migratory insect pests have been subject to this type of management (Pedgley, 1993). However, this type of management may not be possible as many migratory insects have weak control over their flightpaths, partly due to their migrations being multi-generational (Gao et al., 2020). Management actions that change

**Table 3.2**  
Pathway contribution metrics for the full migratory routes in Example 3.3.

Migratory route	Subpopulation pathway contribution metrics				Metapopulation pathway contribution metrics		
	$C(\mathcal{P}_i)$				$\tilde{C}(\mathcal{P}_i)$		
$\mathcal{P}_1$	0	0	0	0	0	0	0
$\mathcal{P}_2$	0	16.1	16.1	0	0	3.43	3.43
$\mathcal{P}_3$	0	8.60	8.60	0	0	1.67	1.67
$\mathcal{P}_4$	0	$7.80 \times 10^{-3}$	$7.80 \times 10^{-3}$	0	0	$1.73 \times 10^{-4}$	$1.73 \times 10^{-4}$
$\mathcal{P}_5$	0	6.18	6.18	0	0	1.19	1.19

the migratory route of individuals have been observed in birds (Hartup et al., 2004), ungulates (Jones et al., 2014) and marine migrants (Perry et al., 2013).

**Example 3.3.** We continue our study of the annual cycle model for the monarch butterfly considered in Example 3.2. Namely, we assess the contribution of various full migratory routes. We set  $\phi = 12$  and  $\Phi = \{1, 2, \dots, 12\}$ ; in other words, all seasons of the annual cycle have a specified pathway.

We calculate the pathway contribution metrics for the following full migratory routes,

$$\begin{aligned}
 \mathcal{P}_1 &:= M \rightarrow M \rightarrow M \rightarrow M \rightarrow S \rightarrow C \rightarrow N \rightarrow C \rightarrow N \rightarrow C \rightarrow M \rightarrow M \rightarrow M, \\
 \mathcal{P}_2 &:= M \rightarrow M \rightarrow M \rightarrow M \rightarrow S \rightarrow S \rightarrow C \rightarrow C \rightarrow C \rightarrow C \rightarrow S \rightarrow M \rightarrow M, \\
 \mathcal{P}_3 &:= M \rightarrow M \rightarrow M \rightarrow M \rightarrow S \rightarrow S \rightarrow C \rightarrow C \rightarrow C \rightarrow S \rightarrow S \rightarrow M \rightarrow M, \\
 \mathcal{P}_4 &:= M \rightarrow M \rightarrow M \rightarrow M \rightarrow S \rightarrow C \rightarrow N \rightarrow N \rightarrow N \rightarrow C \rightarrow C \rightarrow M \rightarrow M, \\
 \mathcal{P}_5 &:= M \rightarrow M \rightarrow M \rightarrow M \rightarrow S \rightarrow S \rightarrow N \rightarrow N \rightarrow N \rightarrow S \rightarrow S \rightarrow M \rightarrow M.
 \end{aligned}
 \tag{3.3}$$

Here,  $\mathcal{P}_1$  is the full migratory route where, for all seasons  $k \in \{1, 2, \dots, 12\}$ , the specified pathway is the pathway with the lowest contribution in season  $k$ , see Table 3.1. On the other hand,  $\mathcal{P}_2$  is the full migratory route where the pathway specified in season  $k$  is the pathway with the highest contribution metric. As in Example 3.2, all the population starts the annual cycle in Mexico (M), so only the first block of  $C(\mathcal{P}_i)$  and  $\tilde{C}(\mathcal{P}_i)$  are populated, hence we only record these values in Table 3.2. Furthermore, when averaging over stage and habitat, only  $\tilde{C}_M(\mathcal{P}_i)$ ,  $\tilde{C}^2(\mathcal{P}_i)$  and  $\tilde{C}^3(\mathcal{P}_i)$  are nonzero and are equal to the nonzero values in the corresponding  $\tilde{C}(\mathcal{P}_i)$ .

Table 3.2 shows that the subpopulation travelling along  $\mathcal{P}_1$  does not contribute to the total population. Further investigation shows that, during October (season 10), the subpopulation does not contain any individuals in habitat C that are in stage 2 or stage 3; hence no individuals use the pathway from  $C \rightarrow M$  during October, as only individuals in stage 2 and 3 use this pathway (see Fig. 3.3). Therefore,  $\mathcal{P}_1$  is not a viable migratory route.

Over all the migratory routes considered presently, we see that individuals travelling along  $\mathcal{P}_2$  contribute the most to the total population, as expected. To increase the total population, managers can increase the proportion of monarch butterflies that use  $\mathcal{P}_2$ .

**Example 3.4.** Here we demonstrate how the habitat contribution metrics, and their maximum values, can play a role in predicting the effect of management actions for populations modelled by (2.1).

Specifically, suppose that, at the start of year  $t$ , members of the population are added via some reintroduction scheme, structured over stage and habitat according to the vector  $\mathbf{u} \in \mathbb{R}_+^{cn}$ . Updating the annual cycle model (2.1) appropriately, the population after one year is then given by

$$\mathbf{x}(t + 1) = \mathcal{A}(\mathbf{x}(t) + \mathbf{u}).$$

In particular, invoking (2.13), we compute that

$$\|\mathbf{x}(t + 1)\|_1 = \mathbf{1}_{cn}^T \mathbf{x}(t + 1) = \mathbf{1}_{cn}^T \mathcal{A}(\mathbf{x}(t) + \mathbf{u}) = \mathbf{C}\mathbf{x}(t) + \mathbf{C}\mathbf{u}, \tag{3.4}$$

where, recall,  $\mathbf{C} = C(\mathcal{P}_0)$  denotes the row vector of habitat contribution metrics. Consequently, it follows from (3.4) that the increase in the size of the population over one year caused by  $\mathbf{u}$  is given by  $\mathbf{C}\mathbf{u}$ . Therefore, for fixed  $\mathbf{x}(t)$ , the size of the population after one year,  $\|\mathbf{x}(t + 1)\|_1$ , is maximised by maximising  $\mathbf{C}\mathbf{u}$ . Evidently,  $\mathbf{C}\mathbf{u}$  increases as  $\|\mathbf{u}\|_1$  increases but, for fixed  $u := \|\mathbf{u}\|_1$ , we see that the maximum of  $\mathbf{C}\mathbf{u}$  is equal to  $\mathbf{H}u$ , where  $\mathbf{H}$  is the largest component of  $\mathbf{C}$ , and the corresponding  $\mathbf{u}$  is equal to  $ue_{n,j}$ . In words, the maximum increase in population is achieved by adding all individuals to the stage and habitat which contributes the most. This choice of management action may not be ecologically practicable, but the above analysis indicates both the theoretical maximum obtainable, and the effect on  $\|\mathbf{x}(t + 1)\|_1$  of other reintroduction schemes.

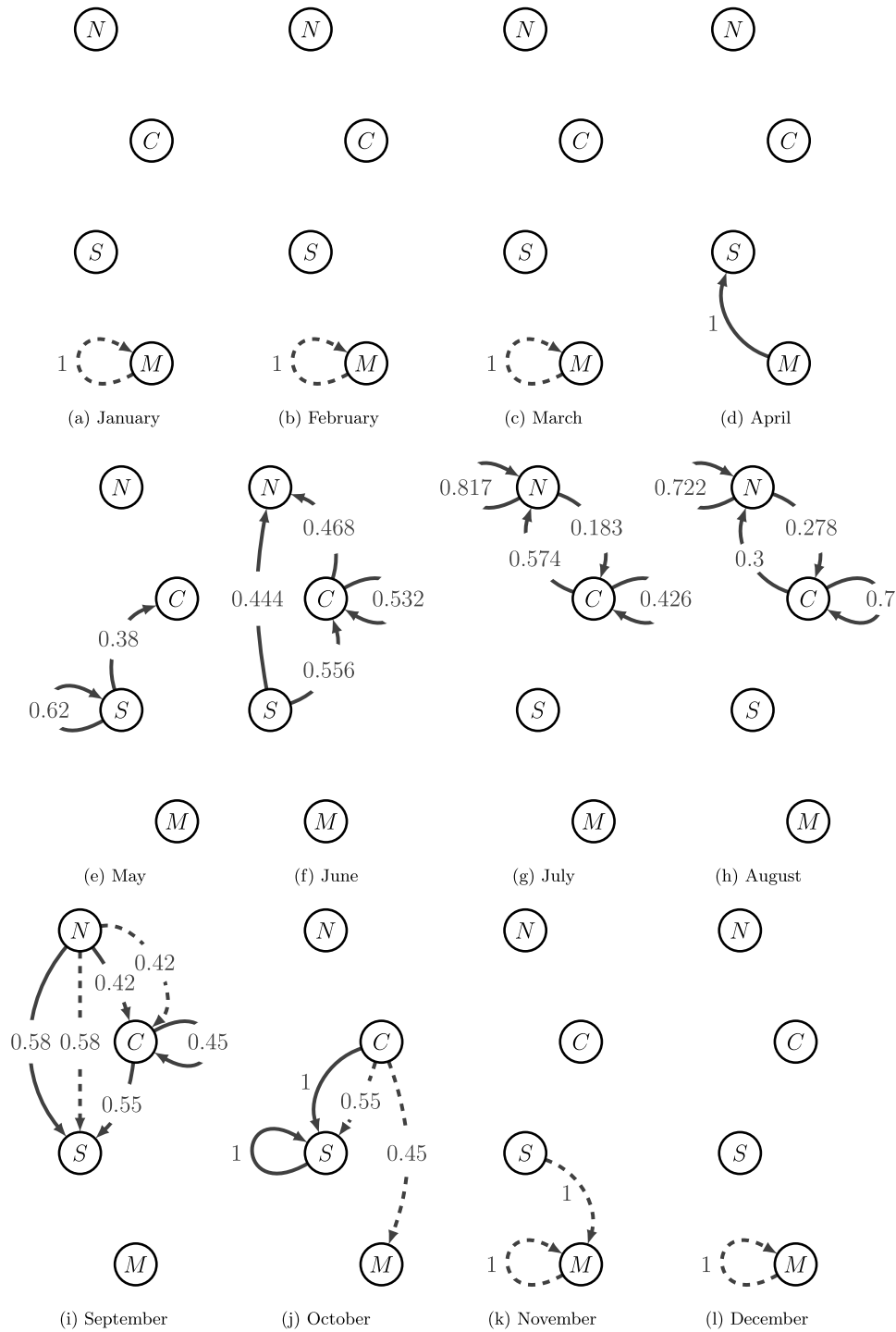
We comment that, adding individuals during a year, say in some other season  $p$ , can be accommodated by rewriting the annual cycle model (2.1) and (2.2) so that the anniversary season is  $p$ .

#### 4. Discussion

We have provided vectorised formulae for two novel pathway contribution metrics to calculate the importance of an individual that travels along specific pathways over any number of prescribed seasons in an annual cycle. Recall the working context that a migratory population is represented by a general so-called annual cycle model — a matrix (structured) population model with discrete temporal and spatial structure. The underlying model and subsequent metrics are presented in Sections 2.2 and 2.3, respectively, and can be applied widely. Our formulae generalise previous frameworks for calculating contribution metrics (Sample et al., 2019; Wiederholt et al., 2018), and familiar habitat contribution metrics are recovered as a special case.

Our approach allows the contribution of any particular part/s of the migratory network to be calculated, including from individuals undertaking a full (annual) migratory route, as well as for models which capture multiple life stages, that is, stage-structured population models. The conjunction of these features is a novel aspect of our work. Using linear algebra methods, we have constructed the contribution metrics such that a pathway of interest can be specified in any season. This allows population managers to focus on particular parts of the migratory network and assess their contributions to the total population. Hence, it is possible to make a detailed analysis of populations with numerous distinct life histories. This provides managers with insights into the role differential migration plays in migratory connectivity and helps to inform conservation actions (Briedis and Bauer, 2018).

Furthermore, our approach can be used to compare, within the same annual cycle, the contributions of the same pathway taken in different seasons (i.e breeding or non-breeding). Previously, this calculation would require a permutation of the annual cycle model; pathway contributions could only be calculated for the anniversary season. Since contribution metrics are transient indices, they are altered by permutations of the annual cycle model. Hence, previous pathway contribution metrics are highly dependent on the anniversary season. It was complicated to compare the contribution of the same pathway used in different seasons. With our metrics, the contribution of a pathway can be calculated for all seasons of the annual cycle, without permuting the annual cycle model. Additionally, our metrics allow managers to see which subpopulations contribute the most to the overall population,



**Fig. 3.3.** Migratory network of monarch butterflies, with four habitats and twelve seasons. Edges are labelled with the transition probabilities. Dashed edges represent stages 2 and 3, solid edges represent stages 4 and 5. This figure is inspired by [Sample et al. \(2019, Fig. 5\)](#).

and distinguish the different contribution rates between life stages in these subpopulations. We have also provided easy to use, vectorised formulae to average the pathway contribution metrics over habitats, and over stages, so that the contribution of all individuals starting in the same stage or habitat can be quantified. These averaged contribution metrics appear in Section 2.7, and are studied in more depth in Smith (2023).

With reference to our case studies from Section 3, for example, in the monarch butterfly study (see Example 3.2) we see that the contribution of an individual that starts the annual cycle in Mexico (M) and stage 2, and migrates from Southern US (S) to Central US (C) in May (season 5) is 1.01—essentially every individual only replaces itself. Whereas an individual that starts the annual cycle in Mexico and stage 2, and migrates from the Southern US to Central US in June (season 6) has a contribution of 13.07. Evidently, the pathway from Southern US to Central US has a much higher contribution in June than it does in May. Then, considering full migratory routes, in Example 3.3, the contribution metrics for five distinct migratory routes are calculated for the monarch butterfly model from Example 3.2. We see that the contribution of an individual in a subpopulation to the total population,  $\tilde{C}(P_i)$ , can range from 0 to 3.43 (Table 3.2). Furthermore, changing the pathway taken in just one season can significantly alter the contribution of an individual —  $P_2$  and  $P_3$  only differ by the pathway taken during season 10 (see (3.3)), however  $\tilde{C}(P_2) = 3.43$  and  $\tilde{C}(P_3) = 1.67$  (Table 3.2). In other words, an individual following  $P_2$  is expected to contribute approximately twice as much to the total population as an individual that follows  $P_3$ , despite using the same pathways for eleven out of twelve seasons of the annual cycle. Arguably, obtaining these insights would not have been possible with previous metrics.

We comment that all the contribution metrics considered are quantities which capture transient behaviour of a population. There has now for some time been a recognition in the academic literature of the importance of transient dynamics in ecological modelling; see, for instance Hastings (2004), Hastings et al. (2018) and Stott et al. (2011). The pathway contribution metrics we have constructed can be considered simultaneously with the habitat contribution metrics and the asymptotic growth rate, as is done in Section 2.6. In particular, there is a connection between transient and asymptotic growth or decline. This connection provides insight into the trade-offs between asymptotic and transient dynamics; increasing the asymptotic growth of the population may not result in short term growth, and vice versa. Insight of these trade-offs allows managers to choose conservation strategies that benefit the population in both the short- and long-term.

By way of limitations, one drawback of our pathway contribution metrics is that by construction they keep track of where individuals are in space but not their stage. As a result, the stage that an individual is in whilst using a migratory pathway is only recorded for the first season of the annual cycle. Therefore, the pathway contribution metrics do not quantify the importance of the stage in which an individual uses a migratory pathway. Instead, the importance of the initial stage of an individual, and the pathways it then uses is quantified. Hence, our metrics do not tell managers which stage of the population to focus conservation actions on for specific pathways of the migratory route. Additionally, our framework is very much geared towards the density-independent (linear) models considered. Indeed, establishing a comparable notion of pathway contribution metrics for full migratory routes for general density-dependent (nonlinear) models seems challenging. Furthermore, the annual cycle model is discrete in nature and so managers are required to make a number of choices when defining the model, including how many stage classes to divide the population into. Matrix models have been criticised for dividing populations into discrete stages despite being classified by continuous traits (Ellner and Rees, 2006). These discretization choices determine the dimension of the matrix which then impacts the outputs of the model and introduces

discretization errors. Much research has been devoted to understanding the effect of these choices on matrix models, including, for example Picard and Liang (2014), Salguero-Gomez and Plotkin (2010); and numerous algorithms that collapse population matrix dimensions, whilst maintaining the intrinsic characteristics of the population, have been proposed for non-spatial population matrices (Bienvenu et al., 2017; Hooley, 2000; Picard et al., 2010). However, to the best of our knowledge, we are unaware of similar algorithms for use on the spatial models considered here. Consequently, at this time we are not able to systematically study the effects of the choice of number of model stages on pathway contribution metrics. We suggest that the development of such algorithms is a fruitful future line of enquiry, to evaluate and quantify discretization errors.

Looking ahead, recent work has considered how existing contribution metrics are affected by perturbations, see Sample et al. (2020). An upcoming work is to provide a modelling framework for perturbations of the contribution metrics considered here (Smith et al., 2022). This could be used to assess the robustness of the population to changes in demographic and migration rates, which can further inform how to apply conservation measures. Another area for future research is to examine how migratory strategies influence the value of contribution metrics. We envisage that this could be studied by specifying a number of annual cycle models with structure corresponding to different migratory strategies (i.e. full migrants or partial migrants) and carrying out a meta-analysis to see if there are significant relationships between the migratory strategy and the corresponding contribution metrics.

In closing, we have provided easy to use formulae for constructing and averaging contribution metrics across stages, and across habitats, in seasonal systems with complex migratory patterns. Our formula are all vectorised, which allows the metrics to be easily calculated from the population projection matrices. These matrices are constructed similarly to standard matrix population models and are based on demographic rates, migratory proportions and migratory survival rates. These results provide another and novel tool for developing improved ecological management strategies.

#### CRedit authorship contribution statement

**Phoebe Smith:** Conceptualization, Methodology, Software, Writing – original draft, Writing – review & editing, Visualization. **Chris Guiver:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Ben Adams:** Conceptualization, Writing – original draft, Writing – review & editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

#### Appendix

The Appendix is divided into five sections. The first contains a mathematical derivation of the equality (2.8). The second compares our per capita subpopulation pathway contribution metrics with the pathway contribution metrics in Sample et al. (2019). The third contains mathematical derivations of the averaged contribution metrics. The fourth and fifth contain further material for Examples 3.1 and 3.2, respectively, not given in the main text.

**Appendix A. Further material for Section 2.2**

We provide a derivation of the equality (2.8), recorded as the following result.

**Lemma A.1.** For every  $k \in \{1, 2, \dots, s\}$ , the matrices  $A_k$  and  $\hat{A}_k$  given by (2.4) and (2.7), respectively, satisfy

$$(A_k)_{xy} = (\hat{A}_k)_{xy} (\mathbb{P}_k)_{xy},$$

where  $\mathbb{P}_k$  is as in (2.5) and  $(A)_{xy}$  represents the  $(x, y)$ th block of  $A$ .

In words, the above lemma states that the  $(x, y)$ th block of the seasonal matrix  $A_k$  is equal to the matrix product of the  $(x, y)$ th block of the seasonal survival matrix  $\hat{A}_k$  and the  $(x, y)$ th block of the block matrix  $\mathbb{P}_k$ , which contains the habitat movement probabilities,  $P_k^i$ .

**Proof of Lemma A.1.** Fix  $k \in \{1, \dots, s\}$ . Recall the definitions of  $A_k$  and  $\hat{A}_k$  in Eqs. (2.4) and (2.7), respectively, namely  $A_k = \mathbb{D}_k \mathbb{M}_k$  and  $\hat{A}_k = \mathbb{D}_k \mathbb{S}_k$ .

Furthermore, recall that the block matrices  $\mathbb{P}_k$ ,  $\mathbb{S}_k$  and  $\mathbb{M}_k$  are constructed via

$$\mathbb{P}_k := \sum_{i=1}^c P_k^i \otimes E_{c,ii}, \quad \mathbb{S}_k := \sum_{i=1}^c S_k^i \otimes E_{c,ii}, \quad \mathbb{M}_k := \sum_{i=1}^c M_k^i \otimes E_{c,ii}.$$

We note that the construction of these block matrices results in each  $c \times c$  block being a diagonal matrix. In particular, the  $(i, i)$ th entry of the  $(x, y)$ th block of  $\mathbb{P}_k$ ,  $\mathbb{S}_k$  and  $\mathbb{M}_k$  is given by the  $(x, y)$ th entry of  $P_k^i$ ,  $S_k^i$  and  $M_k^i$ , respectively. In other words, the  $(x, y)$ th block of  $\mathbb{P}_k$ ,  $\mathbb{S}_k$  and  $\mathbb{M}_k$  are given by

$$(\mathbb{P}_k)_{xy} = \text{diag}_i (P_k^i)_{xy}, \quad (\mathbb{S}_k)_{xy} = \text{diag}_i (S_k^i)_{xy}, \quad (\mathbb{M}_k)_{xy} = \text{diag}_i (M_k^i)_{xy},$$

respectively. We also recall from (2.6) that  $\mathbb{M}_k = \mathbb{P}_k \circ \mathbb{S}_k$ , where  $\circ$  is the Hadamard product.

Collectively, the above gives

$$\text{diag}_i (M_k^i)_{xy} = (\mathbb{P}_k)_{xy} = \text{diag}_i (P_k^i \circ S_k^i)_{xy} = \text{diag}_i P_k^i S_k^i,$$

and so

$$(\mathbb{M}_k)_{xy} = (\mathbb{S}_k)_{xy} (\mathbb{P}_k)_{xy}.$$

We recall that the block matrix  $\mathbb{D}_k$  is constructed via

$$\mathbb{D}_k := \sum_{j=1}^n E_{n,j} \otimes D_{j,k} = \begin{bmatrix} D_{1,k} & 0 & \dots & 0 \\ 0 & D_{2,k} & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \dots & 0 & D_{n,k} \end{bmatrix}.$$

Hence,  $\mathbb{D}_k$  is a block diagonal matrix. Owing to this special structure of  $\mathbb{D}_k$ , we observe that

$$(A_k)_{xy} = (\mathbb{D}_k \mathbb{M}_k)_{xy} = \sum_i (\mathbb{D}_k)_{xi} (\mathbb{M}_k)_{iy} = (\mathbb{D}_k)_{xx} (\mathbb{M}_k)_{xy}.$$

Therefore,

$$(A_k)_{xy} = D_{x,k} (\mathbb{M}_k)_{xy} = D_{x,k} (\mathbb{S}_k)_{xy} (\mathbb{P}_k)_{xy} = \left( \sum_i (\mathbb{D}_k)_{xi} (\mathbb{S}_k)_{iy} \right) (\mathbb{P}_k)_{xy} = (\hat{A}_k)_{xy} (\mathbb{P}_k)_{xy},$$

as required.  $\square$

**Appendix B. A comparison with the pathway contribution metrics of Sample et al. (2019)**

Here, we present a hypothetical annual cycle model to illustrate the connection between our subpopulation pathway metric,  $C(\mathcal{P})$ , and the contribution metrics defined in Sample et al. (2019). There, the authors define a pathway contribution metric as

The annual per-capita contribution of an individual of class  $x$  starting at node  $r$  and travelling to node  $d$  at time  $t$  is

$$C_{rd,t}^x = \frac{\bar{\mathbf{1}}_{nc}^T}{p_{rd,t}^x} \left( (A_t^T \circ (\mathbf{E}_{n,rd} \otimes \mathbf{H}_{c,x})) \left( \prod_{\tau=t+1}^{t+s-1} A_\tau^T \right) \right) \bar{\mathbf{1}}_{nc}, \tag{B.1}$$

where  $\circ$  is the Hadamard (entrywise) product,  $p_{rd,t}^x$  is the proportion of individuals of class  $x$  at node  $r$  that will travel to node  $d$  at time  $t$  (contained in movement matrix  $\mathbf{Q}_t^x$  of Eq. (5)), and  $\mathbf{H}_{c,x}$  is a  $c \times c$  zero matrix with ones in column  $x$ . Recall that  $\mathbf{E}_{n,rd}$  is an  $n \times n$  zero matrix with a 1 at position  $rd$ . (Sample et al., 2019, page 4)

We aim to translate (B.1) into our notation. First, we note that, for simplicity, we assume that seasons are indexed such that the anniversary season is always season 1; hence,  $t = 1$ . Furthermore, we note that the demographic ( $D_{j,k}$ ) and migration ( $M_k^i$ ) matrices we define are the transpose of those defined in Sample et al. (2019, eq(3) and eq(5)). However, our construction of  $\mathbb{D}_k$  and  $\mathbb{M}_k$  results in these matrices being equal to the equivalent matrices in Sample et al. (2019, eq(2) and eq(4)). As a result, when the seasonal matrices  $A_k$  are given by the same product of  $\mathbb{D}_k$  and  $\mathbb{M}_k$ , the annual cycle matrices ( $\mathbf{A}_1$  in Sample et al. (2019, eq(6)) and  $\mathcal{A}$  in our notation) are consistent with each other.

We believe that there is a typo in the order of the subscripts  $r$  and  $d$ ; in our notation, we would use the subscript  $dr$  to denote the pathway from habitat  $r$  to habitat  $d$ . That is, we would denote this pathway contribution as  $C_{dr,1}^x$ , owing to the columns of the matrices denoting where the individual started, whilst the rows indicate where the individual ended up. For the same reasons, we change the order of the subscripts on  $p$  and  $E$ . Furthermore, we believe that  $\mathbf{H}_{c,x}$  in (B.1) should be replaced with  $\mathbf{R}_{c,x}$ , a  $c \times c$  zero matrix with ones in row  $x$ . Making the discussed changes to notation gives

$$C_{dr,1}^x = \frac{\bar{\mathbf{1}}_{nc}^T}{p_{dr,1}^x} \left( (A_1^T \circ (\mathbf{E}_{n,dr} \otimes \mathbf{R}_{c,x})) \left( \prod_{\tau=2}^s A_\tau^T \right) \right) \bar{\mathbf{1}}_{nc}$$

and taking transposes gives

$$C_{dr,1}^x = \frac{\bar{\mathbf{1}}_{nc}^T}{p_{dr,1}^x} \left( \left( \prod_{\tau=2}^s A_\tau \right) (A_1 \circ (\mathbf{E}_{n,rd} \otimes \mathbf{H}_{c,x})) \right) \bar{\mathbf{1}}_{nc}. \tag{B.2}$$

Here,  $A_1 \circ (\mathbf{E}_{n,rd} \otimes \mathbf{H}_{c,x})$  is a  $cn \times cn$  matrix where the  $x$ th column of the  $(r, d)$ th block is equal to the  $x$ th column of the  $(r, d)$ th block of  $A_1$  and all other entries are zero. In other words,  $A_1 \circ (\mathbf{E}_{n,rd} \otimes \mathbf{H}_{c,x})$  is the projection matrix for the first season that projects individuals, that start in stage class  $x$  and habitat  $r$  and travel to habitat  $d$ . Hence,  $C_{dr,1}^x$  is the contribution of individuals that start the annual cycle in stage  $x$  and habitat  $r$  and travel from habitat  $r$  to habitat  $d$  during season 1, if the total population were to travel from  $r$  to  $d$  during the first season.

Adjusting (B.2) to our usual notation we obtain

$$C_r^i(\mathcal{P}) = \frac{\mathbb{1}_{cn}^T}{p_{dr,1}^i} \left( \left( \prod_{\tau=2}^s A_\tau \right) (A_1 \circ (\mathbf{E}_{n,rd} \otimes \mathbf{H}_{c,x})) \right) \mathbb{1}_{cn},$$

where  $\mathcal{P} = r \rightarrow d \not\rightarrow 0 \not\rightarrow \dots \not\rightarrow 0$ , note that this is still only tracking the  $x$ th stage that travel along  $\mathcal{P}_1$ . We use (2.11) to calculate the contribution of all stages along  $\mathcal{P}_1$ , and obtain

$$\begin{aligned} \mathbf{C}(\mathcal{P}) &= \mathbb{1}_{cn}^T \left( \prod_{k=2}^s A_k \right) (\hat{A}_1 \circ (\mathbf{E}_{n,dr} \otimes J_c)) \\ &= [0 \quad \dots \quad 0 \mid \dots \mid C_r^1(\mathcal{P}) \quad \dots \quad C_r^c(\mathcal{P}) \mid \dots \mid 0 \quad \dots \quad 0], \end{aligned} \tag{B.3}$$

where only the  $r$ th  $1 \times c$  vector of  $\mathbf{C}(\mathcal{P})$  is non-zero as we are only tracking individuals that start the annual cycle in habitat  $r$ . Furthermore,  $\hat{A}_1$  is  $A_1$  where each element  $a_{ij}^x$  has been divided by  $p_{ij}^x$ , see Appendix A for proof.

We provide an example to help visualise the difference between (B.1) and (B.3), and that, to the best of our knowledge, the formula (B.1) as presented above does not quite compute what the authors of Sample et al. (2019) claim.

For which purpose, consider an annual cycle model with  $c = 2$ ,  $n = 2$ , and  $s = 1$ . Let the demographic matrices associated with habitat 1 and 2 be given by

$$D_1 = \begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix} \quad \text{and} \quad D_2 = \begin{bmatrix} 0 & 1 \\ 0 & 0 \end{bmatrix},$$

respectively. Furthermore, stages 1 and 2 migrate in the same way, such that

$$M^1 = M^2 = P^1 = P^2 = S^1 = S^2 = \begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix},$$

that is, all individuals migrate from habitat 1 to habitat 2 and all survive.

Then, the seasonal survival matrix,  $\hat{A}$ , and the seasonal matrix  $A$ , are given by

$$A = \hat{A} = A = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

Thus, over the course of the year, which equals a single season, the population projection is

$$\mathbf{x}(t+1) = A\mathbf{x}(t) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} x_1^1(t) \\ x_1^2(t) \\ x_2^1(t) \\ x_2^2(t) \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ x_1^2(t) \\ 0 \end{bmatrix}, \quad (\text{B.4})$$

where  $x_j^i$  denotes the population size in stage  $i$  and habitat  $j$ . Hence, the only state that contributes during time  $t$  is  $x^2(t)$  — individuals starting season  $t$  in stage 2 and habitat 1.

We calculate the contribution of individuals starting the season in stage 2 and habitat 1 that migrate to habitat 2. Therefore, we set  $r = 1$ ,  $d = 2$  and  $i = 2$ .

Using  $A_i^T \circ (E_{n,rd} \otimes H_{c,x})$  from (B.1) (the formula in Sample et al. (2019)) we obtain

$$\begin{aligned} (A^T \circ (E_{n,rd} \otimes H_{c,i})) &= \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}^T \circ \left( \begin{bmatrix} 0 & 1 \\ 0 & 0 \end{bmatrix} \otimes \begin{bmatrix} 0 & 1 \\ 0 & 1 \end{bmatrix} \right) \\ &= \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \circ \begin{bmatrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} = \mathbf{0}. \end{aligned}$$

Hence, we will obtain  $C_{12}^2 = 0$ , and so, this formula calculates that individuals starting the season in stage 2 and habitat 1 that migrate to habitat 2, do not contribute to the next cycle (or season), which we can see is false by (B.4).

Now, using our method, we obtain

$$\begin{aligned} (\hat{A} \circ (E_{n,dr} \otimes J_c)) &= \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \circ \left( \begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix} \otimes \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \right) \\ &= \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \circ \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{bmatrix} = E_{4,32} \neq \mathbf{0}. \end{aligned}$$

Hence,  $C_1^2(\mathcal{P}) = 1$ . Thus, individuals that start the season in stage 2 and habitat 1 and migrate to habitat 2 replace themselves over the annual cycle, as expected from (B.4).

### Appendix C. Averaged contribution metrics

We provide further details not given in Section 2.7, namely, we derive the scalar averaged contribution metrics from the vectorised formulations. We do this for the two forms of averaged contribution metrics separately.

#### C.1. Contribution metrics averaged over stage

Here, we give the derivation of (2.25) from (2.24).

Writing out the various matrices and vectors in (2.24), we see that

$$\begin{aligned} \tilde{\mathbf{H}}(\mathcal{P}) &:= \left( \begin{array}{ccc|ccc} 1 & \dots & 1 & & & \\ & & & \ddots & & \\ & & & & 1 & \dots & 1 \end{array} \right) \\ &\times \left( \begin{array}{c} C_1^1(\mathcal{P})x_1^1 \\ \vdots \\ C_1^c(\mathcal{P})x_1^c \\ \vdots \\ C_n^1(\mathcal{P})x_n^1 \\ \vdots \\ C_n^c(\mathcal{P})x_n^c \end{array} \right) \otimes \left( \begin{array}{ccc|ccc} 1 & \dots & 1 & & & \\ \vdots & & \vdots & & & \\ 1 & \dots & 1 & & & \\ \vdots & & \vdots & & & \\ \vdots & & \vdots & & & \\ & & & \ddots & & \\ & & & & 1 & \dots & 1 \\ & & & & \vdots & & \vdots \\ & & & & 1 & \dots & 1 \end{array} \right) \begin{pmatrix} x_1^1 \\ \vdots \\ x_1^c \\ \vdots \\ x_n^1 \\ \vdots \\ x_n^c \end{pmatrix} \\ &= \left( \begin{array}{ccc|ccc} 1 & \dots & 1 & & & \\ & & & \ddots & & \\ & & & & 1 & \dots & 1 \end{array} \right) \left( \begin{array}{c} C_1^1(\mathcal{P})x_1^1 \\ \vdots \\ C_1^c(\mathcal{P})x_1^c \\ \vdots \\ C_n^1(\mathcal{P})x_n^1 \\ \vdots \\ C_n^c(\mathcal{P})x_n^c \end{array} \right) \otimes \left( \begin{array}{c} \sum_{i=1}^c x_1^i \\ \vdots \\ \sum_{i=1}^c x_1^i \\ \vdots \\ \sum_{i=1}^c x_n^i \\ \vdots \\ \sum_{i=1}^c x_n^i \end{array} \right) \\ &= \left( \begin{array}{ccc|ccc} 1 & \dots & 1 & & & \\ & & & \ddots & & \\ & & & & 1 & \dots & 1 \end{array} \right) \left( \begin{array}{c} (C_1^1(\mathcal{P})x_1^1)/(\sum_{i=1}^c x_1^i) \\ \vdots \\ (C_1^c(\mathcal{P})x_1^c)/(\sum_{i=1}^c x_1^i) \\ \vdots \\ (C_n^1(\mathcal{P})x_n^1)/(\sum_{i=1}^c x_n^i) \\ \vdots \\ (C_n^c(\mathcal{P})x_n^c)/(\sum_{i=1}^c x_n^i) \end{array} \right) \\ &= \left( \frac{\sum_{i=1}^c C_1^i(\mathcal{P})x_1^i}{\sum_{i=1}^c x_1^i} \right) \begin{pmatrix} \vdots \\ \vdots \\ \vdots \end{pmatrix} \in \mathbb{R}_+^n, \end{aligned}$$

which, setting  $x_j = \sum_{i=1}^c x_j^i$ , is the desired expression (2.25)

#### C.2. Contribution metrics averaged over habitat

Here, we give the derivation of (2.27) from (2.26). Writing out the various matrices and vectors in (2.26), we see that

$$\begin{aligned} \tilde{\mathbf{S}}(\mathcal{P}) &= \left( \begin{array}{ccc|ccc} 1 & & & & & \\ & \ddots & & & & \\ & & 1 & \dots & & \\ & & & & 1 & \dots & \end{array} \right) \\ &\times \left( \begin{array}{c} C_1^1(\mathcal{P})x_1^1 \\ \vdots \\ C_1^c(\mathcal{P})x_1^c \\ \vdots \\ C_n^1(\mathcal{P})x_n^1 \\ \vdots \\ C_n^c(\mathcal{P})x_n^c \end{array} \right) \otimes \left( \begin{array}{ccc|ccc} 1 & & & & & \\ & \ddots & & & & \\ & & 1 & \dots & & \\ \vdots & & \vdots & & & \\ 1 & & & & 1 & \dots & \\ & & & \ddots & & \\ & & & & 1 & \dots & 1 \end{array} \right) \begin{pmatrix} x_1^1 \\ \vdots \\ x_1^c \\ \vdots \\ x_n^1 \\ \vdots \\ x_n^c \end{pmatrix} \end{aligned}$$



$$\begin{aligned}
 &= \left( \begin{array}{ccc|ccc} 1 & & & & & \\ & \ddots & & & & \\ & & 1 & & & \\ & & & \cdots & & \\ & & & & & \\ & & & & & 1 \end{array} \right) \left( \begin{array}{c} (C_1^1(\mathcal{P})x_1^1) \\ \vdots \\ (C_1^c(\mathcal{P})x_1^c) \\ \vdots \\ (C_n^1(\mathcal{P})x_n^1) \\ \vdots \\ (C_n^c(\mathcal{P})x_n^c) \end{array} \right) \otimes \left( \begin{array}{c} (\sum_{j=1}^n x_j^1) \\ \vdots \\ (\sum_{j=1}^n x_j^c) \\ \vdots \\ (\sum_{j=1}^n x_j^1) \\ \vdots \\ (\sum_{j=1}^n x_j^c) \end{array} \right) \\
 &= \left( \begin{array}{ccc|ccc} 1 & & & & & \\ & \ddots & & & & \\ & & 1 & & & \\ & & & \cdots & & \\ & & & & & \\ & & & & & 1 \end{array} \right) \left( \begin{array}{c} ((C_1^1(\mathcal{P})x_1^1)/(\sum_{j=1}^n x_j^1)) \\ \vdots \\ ((C_1^c(\mathcal{P})x_1^c)/(\sum_{j=1}^n x_j^c)) \\ \vdots \\ ((C_n^1(\mathcal{P})x_n^1)/(\sum_{j=1}^n x_j^1)) \\ \vdots \\ ((C_n^c(\mathcal{P})x_n^c)/(\sum_{j=1}^n x_j^c)) \end{array} \right) \\
 &= \left( \begin{array}{c} (\sum_{j=1}^n C_j^1(\mathcal{P})x_j^1) \\ \sum_{j=1}^n x_j^1 \\ \vdots \\ (\sum_{j=1}^n C_j^c(\mathcal{P})x_j^c) \\ \sum_{j=1}^n x_j^c \end{array} \right) \in \mathbb{R}_+^c,
 \end{aligned}$$

which, setting  $x^i = \sum_{j=n}^c x_j^i$ , is the desired expression (2.27).

**Appendix D. Further material for Example 3.1**

We provide additional details for Example 3.1 not given in the main text. Namely, we convert the annual cycle model of Wiederholt et al. in Wiederholt et al. (2018) so that migration takes place before demography.

For which purpose, the authors of Wiederholt et al. (2018) split the annual cycle into four seasons: breeding, breeding to non-breeding transition, non-breeding, and non-breeding to breeding transition. Habitats are referred to as seasonally occupied during the origin  $o$ , intermediate  $i$ , or destination  $d$  time periods. Equations are provided for the adult survival probability ( $A^{oid}$ ) and per capita juvenile recruitment ( $J^{oid}$ ) for a focal migratory route  $oid$  during their annual cycle.

$$A^{oid} = s_o^a \cdot s_{oi}^a \cdot s_i^a \cdot s_{id}^a, \tag{D.1}$$

where  $s_o^a$  is the adult survival probability of an individual using habitat  $o$ , and  $s_{oi}^a$  is the survival probability of adults transitioning between habitats  $o$  and  $i$ .

In (D.1), demography is happening before migration. Throughout the paper we have assumed that migration happens first, although we note that the model can be structured such that demography happens first. Hence, here we provide an equation for the adult survival probability ( $A^{oid}$ ) when migration happens before demography. That is,

$$A^{oid} = (s_{oi}^a \cdot s_i^a) \cdot (s_{id}^a \cdot s_d^a).$$

Here, we have used brackets to indicate the split of seasons, noting that, in our framework, this model would be defined as a two season model. In other words, the breeding season and the breeding to non-breeding transition are combined to be one season. Similarly, the non-breeding season and the non-breeding to breeding transition are combined to be one season.

We do similar rearrangements for the per capita juvenile recruitment ( $J^{oid}$ ) equations. We note that the calculation of juvenile survival depends on which season is considered for the anniversary date in the annual cycle (Wiederholt et al., 2018) and consider when anniversary season is the breeding season first. In this case, Wiederholt et al. define

$$J^{oid} = s_o^a \cdot r_o \cdot s_{oi}^j \cdot s_i^j \cdot s_{id}^j,$$

where  $r_o$  is the number of juveniles produced per adult that survives in habitat  $o$ , and  $s_{oi}^j$  is the juvenile survival probability between habitat  $o$

**Table E.1**

Demographic rates.  $s^1$  depends on the season and habitat via  $E_{j,k}$  which is the average number of eggs per milkweed stem in habitat  $j$  during season  $k$ .

Symbol	Definition	Value
$s^1$	Survival of stage 1	$\frac{0.041601(1 + \exp(-1.0175))}{1 + \exp(-1.0175 + 0.1972 \times E_{j,k})}$
$s^2$	Survival of stage 2	0.9896
$s^3$	Survival of stage 3	0.9896
$s^4$	Survival of stage 4	0.56
$s^5$	Survival of stage 5	0.17
$f^4$	Fecundity of stage 4	268
$f^5$	Fecundity of stage 5	89

**Table E.2**

Stage 1 survival.

Month	Habitat			
	Mexico	South	Central	North
January	0.041601	0.041601	0.041601	0.041601
February	0.041601	0.041601	0.041601	0.041601
March	0.041601	0.041601	0.041601	0.041601
April	0.041601	0.041601	0.041601	0.041601
May	0.041601	0.041509	0.041601	0.041601
June	0.041601	0.034856	0.041598	0.041601
July	0.041601	0.041601	0.041007	0.041336
August	0.041601	0.041601	0.016150	0.022597
September	0.041601	0.041601	0.037292	0.035425
October	0.041601	0.041601	0.000076	0.000095
November	0.041601	0.028152	0.041601	0.041601
December	0.041601	0.041601	0.041601	0.041601

and  $i$ . Defining the model such that migration happens first, gives

$$J^{oid} = (s_{oi}^a \cdot s_i^a \cdot r_i) \cdot (s_{id}^j \cdot s_d^j)$$

Secondly, when the non-breeding season is the anniversary season, Wiederholt et al. define the per capita recruitment of juveniles by

$$J^{oid} = s_o^a \cdot s_{oi}^a \cdot s_i^a \cdot r_i \cdot s_{id}^j.$$

Defining the model such that migration happens first, gives

$$J^{oid} = (s_{oi}^a \cdot s_i^a) \cdot (s_{id}^a \cdot s_d^a \cdot r_d).$$

Finally, the pathway contribution is given by  $C^{oid} = A^{oid} + J^{oid}$ , where the order in which migration and demography are defined must be consistent for  $A^{oid}$  and  $J^{oid}$ .

**Appendix E. Further material for Examples 3.2 and 3.3**

We provide further details not given in the main text.

*E.1. Demographic rates*

See Tables E.1–E.3.

*E.2. Migration rates*

See Tables E.4 and E.5.

**Table E.3**

Values used for  $d_j$  and  $e_j$ .

Month	$d_j$				$e_j$			
	Habitat				Habitat			
	Mexico	South	Central	North	Mexico	South	Central	North
January	1	1	1	1	0	0	0	0
February	1	1	1	1	0	0	0	0
March	0	0	0	0	1	1	1	1
April	0	0	0	0	1	1	1	1
May	0	0	0	0	1	1	1	1
June	0	0	0	0	1	1	1	1
July	0	0	0	0	1	1	1	1
August	1	0.25	0.25	0.25	0	0.5	0.5	0.5
September	1	0.5	0.5	0.5	0	0.25	0.25	0.25
October	1	1	1	1	0	0	0	0
November	1	1	1	1	0	0	0	0
December	1	1	1	1	0	0	0	0

**Table E.4**

Matrices encoding the survival of migration of each stage in each season.

Matrices	Stage 1	Stages 2 and 3	Stages 4 and 5
$S_1^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 1.0000 \end{bmatrix}$	<b>0</b>
$S_2^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>
$S_3^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>
$S_4^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0.517 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$S_5^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0.733 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$S_6^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0.733 & 1 & 0 & 0 \\ 0.544 & 0.742 & 0 & 0 \end{bmatrix}$
$S_7^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0.5 & 0 \\ 0 & 0.742 & 1 & 0 \end{bmatrix}$
$S_8^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0.7 & 0.278 & 0 \\ 0 & 0 & 0.3 & 0.722 \end{bmatrix}$
$S_9^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 0.0000 \\ 0.0000.5 \\ 0.0000.5 \\ 0.0000 \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0.567 & 0.5 & 0 \\ 0 & 0 & 1 & 0.5 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$S_{10}^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 0.00196 & 0 \\ 0.00567 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 1 & 0.567 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$S_{11}^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.069 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$	<b>0</b>
$S_{12}^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>

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**Table E.5**

Matrices encoding the proportion of each stage migrating between habitats in each season.

Matrices	Stage 1	Stages 2 and 3	Stages 4 and 5
$P_1^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>
$P_2^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>
$P_3^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>
$P_4^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0.0000 \\ 1.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$
$P_5^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0.62 & 0 & 0 \\ 0 & 0.38 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$P_6^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0.556 & 0.532 & 0 \\ 0 & 0.444 & 0.468 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$P_7^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0.426 & 0.183 & 0 \\ 0 & 0.574 & 0.817 & 0 \end{bmatrix}$
$P_8^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	<b>0</b>	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0.3 & 0.722 & 0 \end{bmatrix}$
$P_9^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 0.0000 \\ 0.0000.58 \\ 0.0000.42 \\ 0.0000 \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0.55 & 0.58 & 0 \\ 0 & 0.45 & 0.42 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$P_{10}^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 0.0000 \\ 0.0000.55 \\ 0.0000 \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$
$P_{11}^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.1000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>
$P_{12}^i$	$\begin{bmatrix} 0.0000 \\ 0.1000 \\ 0.0100 \\ 0.0001 \end{bmatrix}$	$\begin{bmatrix} 1.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix}$	<b>0</b>

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