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Modelling the flowering of four eucalypts species via MTDg with interactions

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Abstract: Phenological indicators (e.g. date of first and last flowering, first arrival of migrating birds) are used as proxies of global climate change (Parry et al. 2008, Hudson et al. 2005; Root et al. 2003). Long-term (1940-1971) synchrony of four Eucalyptus species was recently quantified mathematically at the population-level (Keatley et al. 2004, Kim et al. 2008). Recently Hudson et al. (2009) has identified upper and lower temperature thresholds for *E. leucoxylon* flowering and showed that *E. leucoxylon* flowering is influenced predominantly by minimum temperature whose effect is highly non-linear. Keatley et al. (2002) reported that changes in temperature are likely to translate to changes in flowering commencement time. The magnitude of these shifts (Keatley et al. 2002) is greater than the average reported in meta analysis studies (Root et al. 2003, Parry et al 2008) but in agreement with the results for some individual species in recent studies (Abu-Asab et al 2001, Pẽnuelas et al. 2002, Fitter and Fitter 2002). The aim of this paper is to study the multivariate relationship between the probability of flowering with 2-states of rain and temperature via a mixture transition distribution (MTD) with a different transition matrix from each lag to present (MTDg) analysis (Berchtold 2004). The idea of the mixture transition distribution model is to consider independently the effect of each lag to the present instead of considering the effect of the combination of lags as in pure Markov chain processes. The assumption behind the MTD model, namely the assumed equality of the transition matrices among different lags, is a strong assumption. Earlier studies by Kim et al. (2005, 2008) extended the MARCH software (Berchtold 2004) for MTD modelling of the flowering of four eucalyptus species (as time series). For this current study, an extended model for MTDg (Berchtold 2004) analysis which accommodates interactions was developed. This work extends both MARCH and the work of Kim et al. (2005, 2008) to allow for differing transition matrices amongst the lags, i.e. the MTDg with interaction model. Our model is different to MARCH in terms of incorporating interactions between the covariates and also in its minimization process, namely AD Model Builder^{TM} (Fournier 2000), which uses auto-differentiation as a minimization tool. This is shown to be computationally less intensive than MARCH. We thus developed the MTDg model with interactions model to account for changes in the transition matrices amongst the differing lags. Flowering data were sourced from the Box-Ironbark Forest near Maryborough, Victoria, in particular the flowering records of *E. leucoxylon*, *E. microcarpa*, *E. polyanthemos* and *E. tricarpa* (1940 and 1971). Flowering intensity was calculated by using a rank score (from 0 to 5) based on the quantity and distribution of flowering (Keatley et al. 2004). We used minimum monthly temperature (MinT), maximum monthly temperature (MaxT), mean monthly diurnal temperature (MeanT) and monthly rainfall (Rain) as covariates and their interaction effects in the MTDg model. The MTDg model with interactions showed that the flowering of *E. leucoxylon* and *E. tricarpa* behaves similarly with temperature (both flower at low temperature) and both have a positive relationship with flowering intensity 11 months ago. The flowering of *E. microcarpa* behaves differently in that *E. microcarpa* flowers at high temperature. The MTDg model found a highly significant interaction between two climate variables, mean temperature and rainfall, for *E. polyanthemos*, which commences flowering in January/February but peaks soon after commencement in March. Rain has a direct positive impact on *E. tricarpa* only. The four species studied here are influenced by temperature and rainfall and as a consequence their flowering phenology will change in response to climate change. This in turn will have an impact on species interactions, community structure, and possibly apicultural industry as these species are some of the main producers of honey in Australia.

Keywords: *Eucalypts, flowering, climate, Mixture Transition Distribution (MTD), MTDg*

1. INTRODUCTION

Eucalypts as a genus dominate much of the Australian landscape. Keatley et al. (2002) represents one of the first attempts to utilise Australian phenological data, using more than 30 years of monthly flowering readings to detect responses to climate change. Phenological indicators (e.g. date of first and last flowering, first arrival of migrating birds) are used as proxies of global climate change (Parry et al 2008, Hudson et al. 2005, Root et al. 2003). Long-term (1940-1971) synchrony of four Eucalyptus species was recently quantified mathematically at the population-level (Keatley et al. 2004, Kim et al. 2008). Keatley et al. (2002) reported that changes in temperature are likely to translate to changes in flowering commencement time. The magnitude of these shifts (Keatley et al. 2002) is greater than the average reported in meta analysis studies (Root et al. 2003, Parry et al 2008) but in agreement with the results for some individual species in recent studies (Abu-Asab et al 2001, Pẽnuelas et al. 2002, Fitter and Fitter 2002). Reproductive success may also be influenced by shifts in flowering onset (Hudson et al. 2003). Indeed Keatley and Hudson (1998) showed there is an optimal time for species to flower, depending on bud and fruit volume. Hudson et al. (2008, 2003) identified upper and lower temperature thresholds for *E. leucoxylon* flowering and that the effect of temperature is highly non-linear. It is also worth noting the recent novel work of Kim et al (2008) which combined MTD modelling with the Extended Kalman Filter (EKF) (Julier and Uhlmann (2004)), a method to estimate the past, present and future status of non-linear time series data by minimizing the mean square error using a set of pre-defined mathematical equations. EKF and MTD modelling was combined, in that the functionals and parameterization of a new extended MTD with interactions model, were inputted into the EKF models for the flowering data of the same four eucalypts species analysed here. Kim et al. (2008) adapted Moran's (Moran (1953)) synchronization method to the resultant MTD - EKF residuals. The aim of this paper is to study the multivariate relationship between the probability of flowering (on/off), in relation to two discrete states of rainfall and of temperature (high/low) via a generalized mixture transition distribution (MTD) analysis, which allows for a different transition matrix for each lag (up to 12 months backwards in time) to present flowering, the so-called MTDg analysis (Berchtold 2004). We extend the MTDg model to allow for interactions (between rain and temperature) to account for changes in the transition matrices amongst the differing lags. This work extends both the MARCH MTD software (Berchtold 2004) and the previous work of Kim et al. (2005, 2008).

2. MODELS

Earlier studies by Kim et al. (2005, 2008) extended the MARCH software (Berchtold 2004) for MTD modelling of the flowering records of the same four eucalyptus species and climate time series studied here. For this current study, an extended model for a MTDg (Berchtold 2004) analysis, which accommodates interactions is developed. As in Kim et al. (2008), we develop here, an extended model which accommodates interactions using the AD Model Builder^{TM} (Fournier 2000). This work extends both MARCH and the work of Kim et al. (2005, 2008) to allow for differing transition matrices amongst the lags, i.e. the MTDg with interaction. Our model is different to MARCH in terms of incorporating interactions between the covariates and also in its minimization process, namely AD Model Builder^{TM} (Fournier 2000), which uses auto-differentiation as a minimization tool. This was shown to be computationally less intensive than MARCH (Kim et al, 2008).

2.1. MTDg model

Let $\{Y_t\}$ be a sequence of random variables taking values in the finite set $N = \{1,...,m\}$. In an *l*th-order Markov chain, the probability that $X_t = i_0$, $i_0 \in N$, depends on the combination of values taken by $Y_{t-l},...,Y_{t-1}$. In the basic MTD model, the same transition matrix Q is used to model the relation between any of the lags and the present. The idea of the mixture transition distribution (MTD) model is to consider independently the effect of each lag to the present instead of considering the effect of the combination of lags (Figure 1). as in the case of the more traditional pure Markov chain process (Brémaud, 1999). The constraints imposed by the use of only one transition matrix to represent the relation between each lag and the present is sometimes too strong to allow good modeling of the real high-order transition matrix In this case, it is possible to replace the basic MTD model by a MTDg model. The principle of the MTDg model is to use a different transition matrix of size $(k \times k)$ to represent the relationship between each lag and the present. The high-order transition probabilities are then written as follows,

$$P\left(Y_t = i_0 \mid Y_{t-1} = i_1, \ldots, Y_{t-f} = i_f\right) = \sum_{g=1}^{f} \lambda_g q_{gi_g i_0} \quad (1)$$

where $q_{gi_g i_0}$ is the transition probability from modality i_g observed at time $t-g$ and modality i_0 observed at time t in the transition matrix Q_g associated with the gth lag. In addition to the lag weight vector $\left[\lambda_1, \ldots, \lambda_f\right]$, the MTDg model implies the estimation of f transition matrices $Q_1, \ldots, Q_f$, for a total of $f_k(k-1)+(f-1)$ independent parameters. This is much more than involved in the basic MTD model, but this number of parameters remains small compared to the number of independent parameters of a real fully parameterized *f*th order Markov chain; thus the MTDg and its extensions model prove useful in many situations, as shown in this study.

2.2. MTDg model with interaction

This MTDg model with interactions can also have a different transition matrix of size $(k \times k)$ to represent the relationship between each lag and the present. The high-order transition probabilities are then computed as follows

$$\begin{aligned} &P\left(Y_t = i_0 \mid Y_{t-1} = i_1, \ldots, Y_{t-f} = i_f, C_1 = c_1, \ldots, C_e = c_e, M_1 = m_1, \ldots, M_l = m_l\right) \\ &= \sum_{g=1}^{f} \lambda_g q_{gi_g i_0} + \sum_{h=1}^{e} \lambda_{f+h} d_{hj_h i_0} + \sum_{u=1}^{l} \lambda_{f+e+u} s_{uv_u i_0}, \quad (2) \end{aligned}$$

where λ_{f+e+u} is the weight for the interaction term, $q_{gi_g i_0}$ is the transition probability from modality i_g observed at time t - g and modality i_0 observed at time t in the transition matrix Q_g associated with the gth lag, $s_{uv_u i_0}$ is transition probability between covariate h_1 and covariate h_2 interaction term ($v_u = d_{h_1 j_{h_1}} \times d_{h_2 j_{h_2}}$) and Y_t, and where

$$\sum_{g=1}^{f+e+l} \lambda_g = 1 \quad (3)$$

and

$$\lambda_g \geq 0 \quad (4).$$

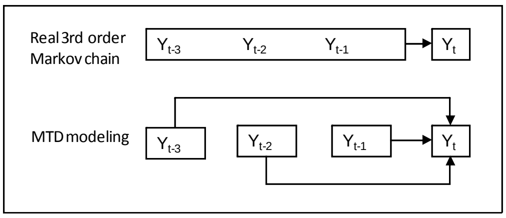

Figure 1. Comparison between a 3rd order Markov chain and its MTD model analogue. In a real high-order Markov chain, the combination of all lags influences the probability of the present. In a MTD model, the contribution of each lag upon the present is considered independently.

2.3. Estimation

The parameters λ and q of the MTD model (2) can be estimated by minimizing the negative the log-likelihood (NLL) of the model:

$$NLL = -\sum_{i_l,\dots,i_0=1}^{m} n_{i_l,\dots,i_0} \log\left(\sum_{g=1}^{f} \lambda_g q_{gi_g i_0} + \sum_{h=1}^{e} \lambda_{f+h} d_{hj_h i_0} + \sum_{u=1}^{l} \lambda_{f+e+u} s_{uv_u i_0} \right) \qquad (5)$$

where $n_{i_l,\dots,i_0}$ is the number of sequences of the form $Y_{t-1} = i_1,\dots,Y_{t-f} = i_f, C_1 = c_1,\dots,C_e = c_e, M_1 = m_1,\dots,$ $M_l = m_l$ in the data. To ensure that the model defines a high order Markov chain, the negative log-likelihood must be minimized with respect to the constraints (3) and (4). ADMB^{TM} was used to minimize the negative the log-likelihood (NLL). This uses auto-differentiation (AUTODIFF) (Fournier, 1996) as a minimization tool, and was shown to be computationally less intensive than MARCH (Kim et al., 2005, 2008). The major advantage of our new model is that its run-time is more than 10 times shorter (less than 1 minute *vs* 2 days) and can be run from a batch file in DOS. Hence multiple models can be tested one after the other in remote mode. The outputs can also be appended into one file to be easily accessed by any graphical software.

3. DATA

Flowering data were sourced from the Box-Ironbark Forest near Maryborough, Victoria, in particular the flowering records of *E. leucoxylon*, *E. microcarpa*, *E. polyanthemos* and *E. tricarpa* (1940 and 1971). Flowering intensity was calculated by using a rank score (from 0 to 5) based on the quantity and distribution of flowering (Keatley et al. 2004, Keatley and Hudson 2007a, Keatley 1999). Flowering intensity scores were dichotomised into two discrete states, namely on and off (1/0) flowering (Figure 2) as in Kim et al. (2005). One temperature variant, of the minimum monthly temperature (MinT), maximum monthly temperature (MaxT) and mean monthly diurnal temperature (MeanT), in addition to the monthly rainfall (Rain) were included as covariates in the MTD and MTDg models; along with the temperature by rain interaction effect. We used discrete state low/high (lower than median temperature *vs* higher than median temperature) for temperature variables and less/more (less than the median rainfall *vs* more than the median rainfall) for the rainfall variable. The cut-points for the states or low/high categories of each covariate are shown in Table 1.

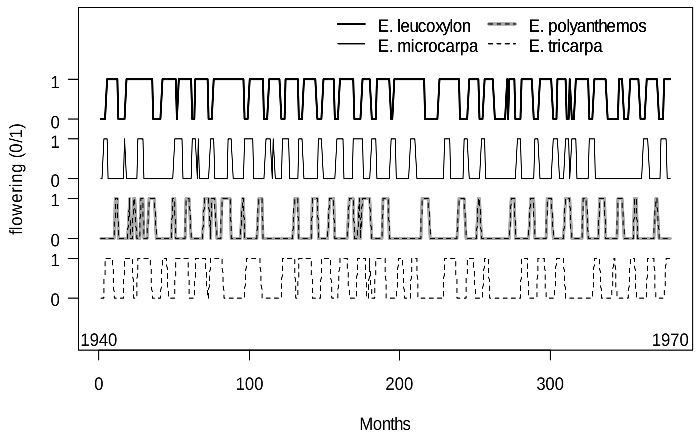

Figure 2. Flowering of four eucalypts species.

Table 1. Cut-points for climate variables based on medians.

Climate variables	Low (less)	High (more)
Min (°C)	≤7.65	>7.65
Max (°C)	≤20.33	>20.33
Mean Diurnal Temp (°C)	≤13.84	>13.84
Rain (mm)	≤40.45	>40.45

4. RESULTS

The MTDg mixing probabilities λ_g and transition probabilities for the four species are given in Table 2. For comparison the analogous results for the MTD model with interactions (of Kim et al., 2005) are reported in Table 3. MTDg modelling showed that flowering intensity of all species was positively and significantly correlated with last month's flowering; with flowering 12 months earlier for *E. polyanthemos* and *E. microcarpa*; and with flowering 11 months earlier for all species except *E. microcarpa* (Table 2). MTDg showed a significant 9 month lag for *E. tricarpa* only. Rainfall was not a significant main predictor of flowering in all species except *E. tricarpa*. Rainfall interacts with temperature for *E polyanthemos* only. MTDg models (Table 2), in agreement with the MTD analysis (Table 3), show that the main temperature driver for *E. tricarpa* is maximum temperature, mean temperature for both *E. leucoxylon* and *E. polyanthemos*; and minimum temperature for *E. microcarpa's* flowering.

Table **2**. Mixing probabilities and transition probabilities of flowering for four species from the MTDg model. "Temp variable" is the relevant temperature variable for each species. Empty cells have zero probabilities.

Species	MTDg model	LL	lag (1) (off,on)	lag (9) (off,on)	lag (11) (off,on)	lag (12) (off,on)
Mic	MinT, rain	-117.61	0.555 (0.01,1.00)			0.300 (0.00,1.00)
Pol	MeanT, rain	-140.69	0.663 (0.05,0.82)		0.186 (0.02,0.97)	0.097 (0.00,0.96)
Leu	MeanT, rain	-122.36	0.616 (0.02,0.99)		0.141 (0.06,1.00)	
Tri	MaxT, rain	-129.54	0.608 (0.00,1.00)	0.053 (0.00,1.00)	0.108 (0.00,1.00)	

Species	Temp variable (low,high)	Rain (less,more)	Temp by rain interaction (low/less,low/more,high/less,high/more)
Mic	0.144 (0.00,1.00)		
Pol			0.046 (0.81,0.00,0.56,1.00)
Leu	0.240 (0.99,0.15)		
Tri	0.165 (1.00,0.00)	0.065 (0.00,1.00)	

Table **3**. Mixing probabilities and transition probabilities of flowering for four species from the MTD model. "Temp variable" is the relevant temperature variable for each species. Empty cells have zero probabilities.

Species	MTD model	LL	lag (1)	lag (9)	lag (11)	lag (12)	Transition probabilities from previous flowering (off,on)
Mic	MinT, rain	115.94	0.544		0.039	0.274	(0.00,1.00)
Pol	MeanT, rain	139.36	0.530	0.060	0.160	0.105	(0.01,1.00)
Leu	MeanT, rain	120.96	0.611		0.124		(0.05,1.00)
Tri	MaxT, rain	129.47	0.609	0.047	0.093		(0.00,1.00)

Species	Temp variable (low,high)	Rain (less,more)	Temp by rain interaction (low/less,low/more,high/less,high/more)
Mic	0.118 (0.00,1.00)		
Pol	0.091 (0.00,0.34)		0.045 (0.88,0.12,0.20,0.96)
Leu	0.202 (1.00,0.00)		
Tri	0.166 (1.00,0.00)	0.064 (0.00,1.00)	

From the MTDg analysis we summarise as follows: Flowering increases as temperature (MinT) increases for *E. microcarpa*, flowering decreases as temperature increases for *E. leucoxylon* and *E. tricarpa* (driven by MeanT and MaxT, respectively). Rainfall positively impacts on the flowering of *E. tricarpa* (i.e. flowering increases with more rainfall). There is a significant interaction between temperature (MeanT) and rainfall on the flowering of *E. polyanthemos* (Table 2). A comparison of the MTDg and MTD analyses show overall similar results. Previous months flowering has a significant positive impact on flowering of the current month for all four eucalypts species, as gleaned by both MTDg and MTD analysis. Flowering at lag 12, the previous year, has a significant positive effect on the flowering of *E. microcarpa* and *E. polyanthemos*, as shown by both MTDg and MTD models. Flowering of 11 months ago has positive effects on flowering of *E. polyanthemos*, *E. leucoxylon,* and *E. tricarpa* from the MTDg models, and on all four species from the MTD analysis. Flowering nine months ago has a significant positive effect on flowering of *E. tricarpa* for both MTDg and MTD; MTD models also found a significant 9 month lag for *E. polyanthemos*.

5. DISCUSSION AND CONCLUSIONS

In conclusion, the MTDg model with interactions shows that the flowering of *E. leucoxylon* and *E. tricarpa* are influenced similarly by temperature (both flower at low temperature) and exhibit a positive relationship with flowering 11 months ago. For *E. leucoxylon* this is because it has two months in which flowering commencement is almost equally likely: April and June, 0.36 and 0.39, respectively (Keatley and Hudson 2007a). The reason is less clear for *E. tricarpa* as the probability of flowering commencement 11 months prior is low, 0.04. The flowering of *E. microcarpa* behaves differently from *E. leucoxylon* and *E. tricarpa*. *E. microcarpa* flowers at high temperature and its flowering has a significant and positive relationship with flowering a year ago. This illustrates this species is more consistent as to when it starts flowering (i.e. *E. microcarpa* has a probability of commencing flowering 12 months before of 0.67 compared to *E. leucoxylon* and *E. tricarpa*, respectively 0.41 and 0.39) (Keatley and Hudson 2007a). The MTDg model found a significant interaction between two climate variables, mean temperature and rainfall on the flowering of *E. polyanthemos*. As flowering is viewed as either "off" or "on" this interaction appears to be delineating *E. polyanthemos'* flowering period. It usually commences flowering in late spring - as mean temperature is increasing and rainfall is decreasing and ceases in early summer; just prior to the warmest mean temperature and lowest rainfall. An alternative interpretation of this interaction could also be that as flowering is viewed as either "off" or "on" it is delineating the climate profile during *E. polyanthemos'* flowering period. These species are influenced by temperature (Keatley et al. 2002) and in some instances rainfall and as a consequence their flowering phenology will change in response to climate change. These changes can be regarded as the short-term impacts of climate change (Rehfeldt et al. 2004). The longer-term consequences are changes in their individual reproductive success and distribution. These changes in phenology to climate change will in turn have an impact on other species (e.g. 20% of vertebrate species are nectar dependent Traill 1991), and possibly apicultural industry as these species are some of the main producers of honey in Australia (Victorian Environment Assessment Council 2001) and therefore changes in flowering would have significant economic consequences. Future work will entail the modification of the MTD and MTD***g*** models discussed here to incorporate all the three temperature variants, rainfall main effects and their interactions. Multivariate MTD (M-MTD) models are also the topic of future work. It is anticipated that our M-MTD models (with a multiplicity of covariates) may be more sensitive than MTD and MTDg models in establishing temperature by rainfall interactive effects on flowering. Indeed the influence of rain on these species needs further examination as its effect has been shown to range from none (Porter 1978; Keatley and Hudson 2000) to a significant but minor effect (i.e. temperature has a much greater influence) (Wells 2000; Keatley et al. 2002); to significant with a major influence (Wilson and Bennett 1999; Kim et al. 2005). Given these mixed results indications are that, as in semi-arid woodlands, there is a rainfall threshold required before flowering can occur (Hodgkinson and Freudenberger 1997).

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