QUANTIFYING THE IMPACT OF GLOBAL CLIMATE CHANGE ON POTENTIAL NATURAL VEGETATION

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Abstract. Impacts of climate change on vegetation are often summarized in biome maps, representing the potential natural vegetation class for each cell of a grid under current and changed climate. The amount of change between two biome maps is usually measured by the fraction of cells that change class, or by the kappa statistic. Neither measure takes account of varying structural and floristic dissimilarity among biomes. An attribute-based measure of dissimilarity (ΔV) between vegetation classes is therefore introduced. ΔV is based on (a) the relative importance of different plant life forms (e.g. tree, grass) in each class, and (b) a series of attributes (e.g. evergreen-deciduous, tropical-nontropical) of each life form with a weight for each attribute. ΔV is implemented here for the most used biome model, BIOME 1 (Prentice, I. C. et al., 1992). Multidimensional scaling of pairwise ΔV values verifies that the suggested importance values and attribute weights lead to a reasonable pattern of dissimilarities among biomes. Dissimilarity between two maps ($\Delta \mathbf{V}$) is obtained by area-weighted averaging of ΔV over the model grid. Using $\Delta \mathbf{V}$, present global biome distribution from climatology is compared with anomaly-based scenarios for a doubling of atmospheric CO_2 concentration ($2 \times CO_2$), and for extreme glacial and interglacial conditions. All scenarios are obtained from equilibrium simulations with an atmospheric general circulation model coupled to a mixed-layer ocean model. The $2 \times CO_2$ simulations are the widely used OSU and GFDL runs from the 1980's, representing models with low and high climate sensitivity, respectively. The palaeoclimate simulations were made with CCM1, with sensitivity similar to GFDL. $\Delta \mathbf{V}$ values for the comparisons of $2 \times CO_2$ with present climate are similar to values for the comparisons of the last interglacial and mid-Holocene with present climate. However, the two simulated $2 \times CO_2$ cases are much more like each other than they are to the simulated interglacial cases. The largest $\Delta \mathbf{V}$ values were between the last glacial maximum and all other cases, including the present. These examples illustrate the potential of $\Delta \mathbf{V}$ in comparing the impacts of different climate change scenarios, and the possibility of calibrating climate change impacts against a palaeoclimatic benchmark.

1. Introduction

Global biome maps have been widely used to assess the impacts of simulated past and future climate change on ecosystems (e.g. Prentice et al., 1993; Neilson, 1995; Prentice and Sykes, 1995). Biome distributions are typically simulated using equilibrium biogeography models, also called biome models (Prentice et al., 1992; VEMAP Members, 1995; Haxeltine and Prentice, 1996). Such models use different combinations of a small number of plant functional types (PFTs) and climatic

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variables to simulate the distribution of a number of discrete vegetation classes or 'biomes', which are defined as large-scale vegetation units characterized by the predominance of one or more PFTs. When applied to climate scenarios for the next centuries, these equilibrium model results describe the *potential* vegetation, i.e. the vegetation type towards which the natural (non-modified) vegetation would develop under a simulated climate, rather than the actual (modified) vegetation. Transient responses of vegetation to continuing changes in climate can be simulated with dynamic global vegetation models (e.g. Foley et al., 1996), but these are still under development, and not yet widely used in impact studies.

Assessments of the magnitude of climatically induced change from one simulated global biome map to another has often been based on visual comparisons. Quantification is however both possible and useful. An obvious quantitative measure is the simple fraction of grid cells that show different biomes in the two maps (e.g. Claussen, 1994). Recently, the kappa statistic (Cohen, 1960; Landis and Koch, 1977; Monserud and Leemans, 1992; Neilson, 1993; Haxeltine and Prentice, 1996) has also become popular for this purpose. The kappa statistic is derived from the fraction of grid cells that remain the same between two maps, but this fraction is corrected to allow for the fraction that would be expected to remain the same between two random maps with the same class frequencies. Although formal statistical testing is inappropriate, there is an accepted subjective scale for interpreting values of kappa, ranging from 'no agreement' to 'perfect agreement' (Monserud and Leemans, 1992). As this terminology implies, the kappa statistic is well suited to assessing the *degree of similarity* between two maps that are expected a priori to agree. The kappa statistic has been used in this way to assess the similarity between simulated and observed vegetation maps (Prentice et al., 1992; VEMAP Members, 1995; Haxeltine and Prentice, 1996).

The interpretation of the kappa statistic is less obvious when the aim is to quantify the *amount of change* between two maps derived using the same model. Here the question of how many grid cells would stay the same under randomization is not relevant. A further problem, which affects both the simple fractions and the kappa statistic, is that all biome changes are treated as equivalent. This is undesirable in a measure designed to quantify vegetation change. To take an extreme example, consider two grid cells occupied by boreal forest. The first changes to a mixed (coniferous-deciduous) forest, the second to a tropical savanna. We suggest that the second change should contribute more to a measure of dissimilarity than the first.

A related difficulty is that with increasing impacts, the simple fractions and the kappa statistic 'saturate' when all the grid cells have changed. We suggest that a measure of dissimilarity should continue to increase, as extant vegetation types are replaced by types that have less and less structurally and floristically in common.

We therefore need a non-trivial measure of *dissimilarity between biomes*, i.e. a measure that takes values other than the values 0 and 1 that are implied in the simple fraction and in the kappa statistic. That is what is done in this paper. Such a measure

can be spatially averaged in order to yield an overall measure of the change between two maps. We illustrate the use of our proposed measure by applying it to biome simulations representing a range of past, present and future (high greenhouse gas concentration) conditions.

2. Methods

2.1. DISSIMILARITY BETWEEN BIOMES

Here we develop the dissimilarity measure between biomes, ΔV, and its implementation in the context of BIOME 1 (Prentice et al., 1992). We focus on BIOME 1 because it is well known, because it has been applied more widely than any other biome model (apart from the earlier, non-mechanistic models such as the Holdridge scheme, which does not lend itself to biological interpretation in terms of plant life forms and attributes), and because of its relative simplicity.

We define:

$$\Delta V(i, j) = 1 - \sum_k \{\min(V_{ik}, V_{jk}) * [1 - \sum_l w_{kl}|a_{ikl} - a_{jkl}|]\}, \tag{1}$$

where $\Delta V(i, j)$ is the dissimilarity between biomes i, j; V_{ik}, V_{jk} are the importance values of plant life-form k in biomes i, j; a_{ikl}, a_{jkl} are the values of attribute l for plant life form k in biomes i, j; w_{kl} is a weight for attribute l of plant life form k.

It is assumed that both the importance values and the attribute values are all in the range from 0 to 1; that the sum of importance values for each biome, $\sum_k V_{ik} = 1$ (this means in practice that we must define a dummy life form called 'bare ground', e.g. to distinguish deserts from closed vegetation types); and that the sum of weights, $\sum_l w_{kl} \leq 1$. If no attributes are defined for a given plant life form, the term in square brackets is set to 1.

Equation (1) can be understood by considering first the similarity index $\sum_k \min(V_{ik}, V_{jk})$. This index reflects only differences in plant life form composition. It takes the value 0 if and only if the two biomes are identical in plant life form composition, and 1 if and only if they have no plant life forms in common. In Equation (1), the terms of this simple index are each multiplied by a reduction factor (the term in square brackets). This factor depends on the attributes of the plant life form involved, for example, whether or not the trees are evergreen. If the attributes of a given plant life form are the same in both biomes then the reduction factor becomes 1, i.e. similarity is not reduced. If the attributes are completely different and the sum of the weights is 1, then the reduction factor becomes zero and the plant life form in question contributes nothing to similarity. The resulting similarity index also ranges from 0 in the case of identity, to 1 in the case of complete contrast. Subtraction from 1 converts this similarity measure to the dissimilarity index ΔV.

TABLE I

Importance values for plant life forms in each biome

Biome	Life form		
	Trees	Grass/shrub	Bare ground
Forests	1		
Tropical dry forest/			
savanna	0.75	0.25	
Xeric woods/scrub	0.50	0.50	
Grass/shrub		1	
Deserts		0.25	0.75
Tundra		1	

Implementation of ΔV requires the definition of plant life forms, assignment of importance values for life forms, definition of attributes, assignment of attribute values, and assignment of attribute weights.

The definitions of plant life forms and attributes follow naturally from the structure of the model. They could be different for different models, depending on what aspects of vegetation structure the model predicts. For example, BIOME 1 does not predict the distribution of grasses versus shrubs, so for this implementation we define only trees, grasses/shrubs, and bare ground as the three plant life forms.

The importance values and attribute values that we have used in our implementation of the method for BIOME 1 are given in Tables I and II. These values represent rough estimates of the dominance of different types of plant in each of the biomes. For example, forests are dominated by trees (hence the life form 'trees' is given an importance value of 1); deserts are dominated by bare ground with some amount of grass/shrub (hence 'grass/shrub' is given an importance value of 0.25 while 'bare ground' gets 0.75); and so on. Further information is added by way of the importance values, so that, for example, the trees in tropical rainforest are tropical evergreen broad-leaved and therefore are assigned attribute values of 1 for evergreen, 0 for needle-leaf, 1 for tropical, 0 for boreal; the trees in taiga are mainly boreal evergreen needle-leaved but with some boreal deciduous broad-leaved or needle-leaved, so they are assigned attribute values of 0.75 for evergreen and needle-leaved, 0 for tropical, 1 for boreal. These assignments are necessarily rough and somewhat subjective; however, it is unlikely that different ecologists would assign greatly differing values.

Note that in suggesting the weights in Table II, we imposed the additional constraint that the sum of attribute weights, $\sum_l w_{kl} = 1$. This constraint amounts to giving approximate parity to attribute distinctions and life form distinctions.

The weights for attributes are explicitly subjective. This is unavoidable because there is no obvious a priori basis for assigning relative significance to, say, leaf

TABLE II

Attribute values and weights for plant life forms

Life form	Attribute			
Trees:	Evergreen	Needle-leaf	Tropical	Boreal
Tropical rain	1	0	1	0
Tropical seasonal	0.75	0	1	0
Tropical dry/savanna	0	0	1	0
Broad-leaf evergreen/				
warm-mixed	0.75	0.25	0	0
Temperate deciduous	0.25	0.25	0	0
Cool mixed	0.5	0.5	0	0.5
Cold mixed	0.5	0.5	0	0
Cool conifer	0.75	0.75	0	0.75
Taiga	0.75	0.75	0	1
Cold deciduous	0	0.5	0	1
Xeric woods/scrub	1	0.5	0	0
(Weights	0.2	0.2	0.3	0.3)
Grass/shrub:	Warm	Arctic/alpine		
Tropical dry/savanna	1	0		
Xeric woods/scrub	0.75	0		
Warm grass/shrub	1	0		
Hot desert	1	0		
Polar desert	0	1		
Tundra	0	1		
(Weights	0.5	0.5)		
Bare ground:	Permafrost			
Polar desert	1			
Others	0			
(Weight	1)			

size versus phenological characteristics, or any of these characteristics versus the major differences in plant life form composition. In Table II, we have assigned equal weights to logically comparable attributes (e.g. tropical and boreal) and we have weighted the 'climatic' tree attributes tropical and boreal somewhat higher than the attributes describing leaf size and phenology.

In order to check the reasonableness of the set of values listed in Tables I-II, we approximated the structure of the resulting pairwise matrix of ΔV values between biomes in three dimensions using non-metric multidimensional scaling (NMDS) (Kruskal, 1964; Prentice, 1977). This representation indicates visually which biomes are considered relatively similar and which relatively different, given the particular weights we assigned. NMDS iterates from a random initial configuration to approach an optimum configuration in which the distances between points in a space of specified dimensionality approximate, as closely as possible, a monotonic relationship with the underlying pairwise dissimilarity values. Deviation from monotonicity is measured by a 'stress' statistic ranging from 0 (perfect agreement) to 1 (no relationship). NMDS was implemented using Kruskal's least-squares monotone regression algorithm (Podani, 1994).

2.2. DISSIMILARITY BETWEEN MAPS

Having defined ΔV for biomes, it is then straightforward to calculate an overall measure (which we distinguish as $\Delta \mathbf{V}$) by averaging over the grid:

$$\Delta \mathbf{V} = \sum_h W_h \Delta V_h / \sum_h W_h \,, \tag{2}$$

where $\Delta \mathbf{V}$ is the overall dissimilarity between two biome maps; ΔV_h is the value of ΔV at grid cell h; W_h is a weighting factor for grid cell h.

With a regular latitude-longitude grid as used here, equal-area weighting is achieved by setting W_h to be equal to the cosine of latitude. Area weighting factors could equally well be applied to non-regular grids or polygons, if the application demanded this.

2.3. BIOME AND CLIMATE MODEL EXPERIMENTS

As a baseline for comparisons, we used the biome distribution as simulated by BIOME 1 using the Leemans and Cramer (1991) climate dataset (updated version supplied by W. Cramer, personal communication, 1995) on a 0.5° global grid (Figure 1). Changed-climate scenarios were based on published applications of BIOME 1. In all of these application, scenarios were derived using a standard method based on equilibrium simulations of an atmospheric general circulation model (AGCM) coupled to a mixed-layer ocean model with fixed horizontal heat transport. Anomalies (differences between the climate model 'experiment' and control run) of simulated mean monthly temperature and precipitation were interpolated from the coarser AGCM grid to the 0.5° grid, and added to the baseline climatology. The resulting modified climatology was used to drive a simulation

Figure 1 (facing page). Global biome maps using BIOME 1: Top – using a Last Glacial Maximum climate; Middle – under present day climate; Bottom – a future climate (GFDL).
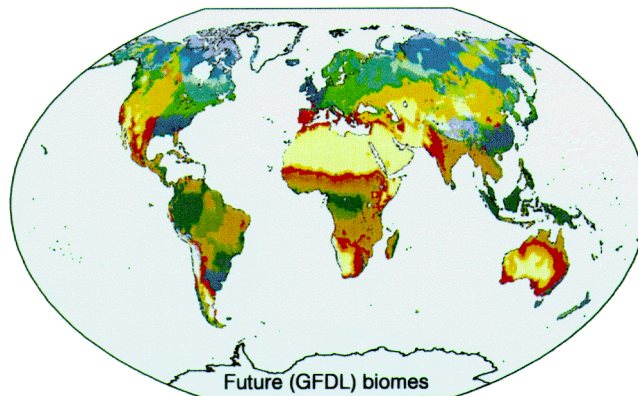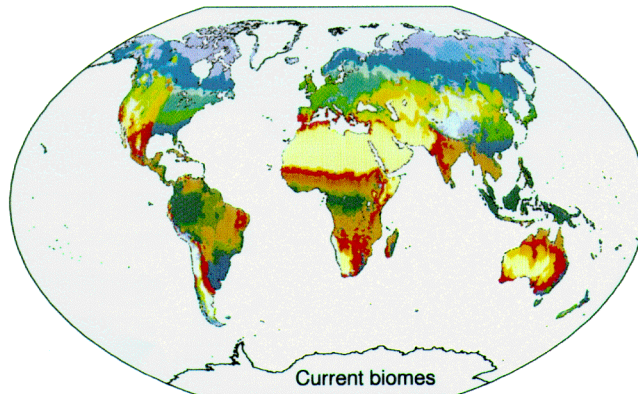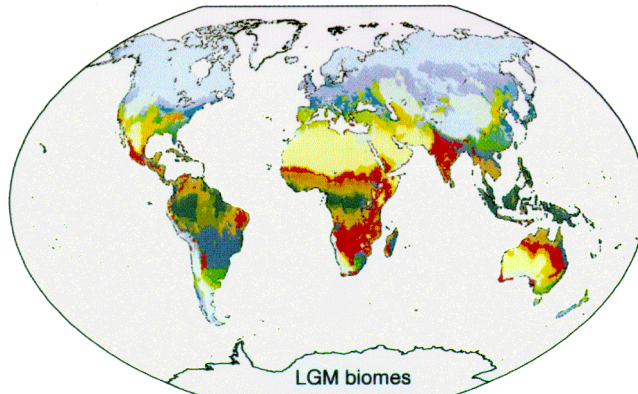
LGM biomes

Current biomes

Future (GFDL) biomes

Cool Grass/Shrub	Warm Grass/Shrub	Tropical Dry Forest/Savanna
Cold Deciduous Forest	Evergreen/Warm mix Forest	Tropical Seasonal Forest
Taiga	Temperate Deciduous Forest	Tropical Rain Forest
Tundra	Cool Mixed Forest	Xerophytic Woods/Scrub
Semidesert	Cold Mixed Forest	Hot Desert
Polar Desert	Cool Conifer Forest	

with BIOME 1. Finally we calculated $\Delta\mathbf{V}$ between each of these changed-climate simulations and the baseline simulation.

The 'future' simulations used were the OSU (Schlesinger and Zao, 1989) and GFDL (Manabe and Wetherald, 1987) runs, with atmospheric CO_2 concentration raised to twice its pre-industrial level (Figure 1). These two climate models were chosen because they have been extensively used in climate impact studies and because they represent approximately the lower and upper bounds, respectively, for the 'climate sensitivity', i.e. the sensitivity of simulated global mean temperature to the radiative forcing implied by a doubling of CO_2 (Houghton et al., 1990). The palaeoclimate simulations were all made using the NCAR CCM1, which has a climate sensitivity similar to that of GFDL (Gates et al., 1992). The following palaeoclimate simulations were used:

- The **P+T+** simulation (Harrison et al., 1995), represents the 'peak interglacial' configuration of the Earth's orbit, with the maximum potential for high-latitude warming that has occurred during the Late Quaternary. This potential was nearly achieved during the early part of the last (Eemian) interglacial around 126 ka (1 ka = 1000 years before present). Atmospheric CO_2 concentration was set equal to the modern control run, consistent with the Vostok ice-core measurements (Barnola et al., 1987) showing CO_2 concentration reaching a peak approaching modern values around 126 ka.

- The **6 ka** simulation (Kutzbach et al., 1998), represents a smaller though qualitatively similar orbital forcing, as experienced during the mid-Holocene. During the current glacial-interglacial cycle, the insolation anomaly was maximal around the beginning of the Holocene, but the North American ice sheet took several thousand years to disappear. As a result, maximum warmth in regions 'downstream' did not occur until around 6 ka (Harrison et al., 1992; Huntley and Prentice, 1993). Atmospheric CO_2 equivalent was set at 280 ppm, consistent with ice-core measurements showing little or no change from 6 ka through to the immediate pre-industrial period.

- The **LGM** simulation (Kutzbach et al., 1998) represents conditions at the last glacial maximum, ca. 21 ka (Figure 1). At this time, although the Earth's orbit was not very different from present, the ice sheets (thanks to the accumulated effects of earlier low-insolation periods) were close to their maximum extent and concentrations of CO_2 and other greenhouse gases were close to their lowest Quaternary levels. In addition to the minor orbital change, ice-sheets and sea-level were prescribed consistent with Peltier (1994) and atmospheric CO_2 concentration was set to 200 ppm based on the ice-core measurements. $\Delta\mathbf{V}$ was calculated in two ways in this case: points occupied by ice at the LGM were either considered as polar desert, or excluded from comparison. Points that formed part of the exposed continental shelf at the LGM (e.g. the Sunda Shelf; see e.g. Prentice et al., 1993) were excluded from comparison.

These various palaeoclimate model runs can thus be considered to bracket the range of climatic forcing conditions that has been experienced by the Earth during approximately the past million years.

3. Results

3.1. DISSIMILARITY BETWEEN BIOMES

The NMDS analysis reached a stress level of 0.11 after 30 iterations. This is within the range 0.1–0.2 considered as 'satisfactory' (Podani, 1995). Inspection showed that the relationship between distances and dissimilarities in the final configuration (Figure 2) was approximately proportional, so the distances in Figure 2 can be treated as a simple reflection of ΔV.

The configuration shown in Figure 2 seems appropriate to describe differences among biomes. The axis 1 separates treeless (desert, steppe and tundra) biomes from forested biomes, with xerophytic vegetation and dry forest/savanna appropriately intermediate. Differences between biomes closely associated on axis 1 are expressed in axis 2, which mainly shows a temperature-related gradient, both among the forests and among the non-forests. Axis 3 distinguishes deserts from other treeless biomes, and further accentuates the difference between tropical and non-tropical forests. Overall, there are large variations in the ΔV values calculated for different pairs of biomes. For example, certain types of temperate forest (temperate deciduous, broad-leaved evergreen/warm mixed, and cool mixed) are considered very similar; this is reasonable because many species and genera run across the boundaries and because the structure of all of these types is rather similar, with a closed canopy of moderate height consisting of some mixture of broad-leaved and needle-leaved trees. Forest types at the extreme of the thermal gradient (cold deciduous forest and tropical rain forest) are considered substantially different, which is reasonable because they have no species or genera in common and are structurally very different. The largest differences are between forests and treeless vegetation.

The fact that BIOME 1 distinguishes more temperate than tropical biomes probably reflects the fact that it was devised by ecologists from temperate climates. The ΔV values correct for this bias, by not giving undue weight to changes among temperate biomes.

3.2. DISSIMILARITY BETWEEN MAPS

Table III show the global $\Delta \mathbf{V}$ values (area-weighted averages across grid cells) for comparisons between changed-climate and baseline simulations with BIOME 1. The largest value by far (i.e., the biome distribution differing most from the present one) was for the LGM simulation, even when the then ice-covered areas were excluded from comparison. Next largest was for the P+T+ (maximum interglacial)
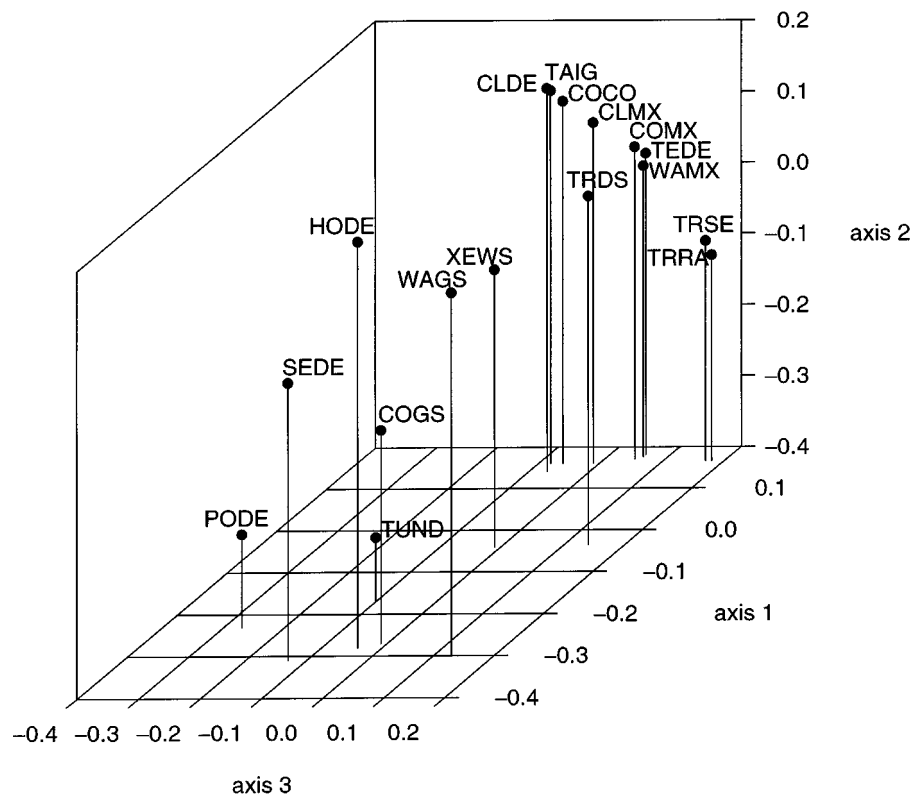
Figure 2. A non-metric multidimensional scaling ordination (3D plot) of the ΔV values for the 17 BIOME 1 biomes. CLDE, cold deciduous forest; CLMX, cold mixed forest; COCO, cool conifer forest; COGS, cool grass/shrub; COMX, cool mixed forest; HODE, hot desert; PODE, polar desert; SEDE, semi-desert; TAIG, taiga; TEDE, temperate deciduous forest; TRDS, tropical dry forest/savanna; TRRA, tropical rain forest; TRSE, tropical seasonal forest; TUND, tundra; WAGS, warm grass/shrub; WAMX, broad-leaved evergreen/warm mixed forest; XEWS, xerophytic woods/scrub.

simulation, followed by the 6 ka simulation; however, the values for these two interglacial simulations are only slightly greater than those for the two $2 \times CO_2$ simulations. Thus, these results suggest that the simulated impacts of CO_2 doubling on biome distribution are of roughly comparable magnitude to the impacts of the change between peak-interglacial and modern climates. Among the $2 \times CO_2$ simulations, ΔV for the GFDL simulation was somewhat larger than that for the OSU simulation, consistent with the ranking of the two models' sensitivities to atmospheric CO_2 concentration.

It is at first sight surprising that the ΔV between the P+T+ simulation and the baseline simulation is only slightly greater than the ΔV between the 6 ka simulation and the baseline simulation, given the large high-latitude changes (compared to 6 ka) that were shown by Harrison et al. (1995) and the abundant palaeoecological

TABLE III

Calculated ΔV values (comparisons with present)

	ΔV
Palaeoclimate:	
LGM	0.445, 0.377[a]
P+T+	0.229
6 ka	0.212
$2 \times CO_2$ climate:	
GFDL	0.210
OSU	0.173

[a] Excluding areas that were ice-covered at the LGM.

TABLE IV

Calculated ΔV values for 30° latitudinal sections of the globe (comparisons with present)

	6 ka	P+T+
90° N–60° N	0.215	0.371
60° N–30° N	0.218	0.238
30° N–0°	0.238	0.266
0°–30° S	0.164	0.112
30° S–60° S	0.187	0.070

evidence for larger high-latitude warming at 126 ka than at 6 ka. However, a latitudinal breakdown (Table IV) shows that the greatest biome changes between P+T+ and modern are just in the high northern latitudes. In the southern hemisphere, the changes between P+T+ and modern are less than the changes since 6 ka. At a global scale these differences almost cancel.

It is also instructive to analyse pairwise $\Delta\mathbf{V}$ values among all simulations (Table V). The largest differences are, not surprisingly, between the LGM and the 'warm climate' simulations (interglacial and $2 \times CO_2$). Next largest is the value between LGM and the present day. However, the differences between interglacial simulations and $2 \times CO_2$ simulations are consistently larger than the difference between the two interglacial simulations, the difference between the two $2 \times CO_2$ simulations, and the differences between the 'warm climate' simulations and present. In other words, the two $2 \times CO_2$ simulations – even though they are based on

TABLE V

Calculated ΔV across all climates

	LGM	6 ka	GFDL	OSU	Present
P+T+	0.529	0.203	0.241	0.259	0.229
LGM		0.507	0.497	0.487	0.443
6 ka			0.273	0.241	0.212
GFDL				0.124	0.210
OSU					0.173

climate models with different climate sensitivity – produce quite similar biome shifts, which are different in character from the shifts generated by the change in orbital forcing from peak-interglacial conditions to present.

4. Discussion

The two $2 \times CO_2$ simulations yielded different ΔV values, consistent with the ranking of the climate models' reported sensitivities to radiative forcing. However, the differences in $\Delta \mathbf{V}$ between the two models are not proportional to these sensitivities. In this case the models differ less in their implications for biome distributions than they do in their global mean temperature response. Furthermore, the biome shifts generated by these two models are similar, yielding the smallest of all pairwise $\Delta \mathbf{V}$ values. In contrast, $\Delta \mathbf{V}$ values between the $2 \times CO_2$ simulations and the two interglacial simulations are larger than the differences between either type of simulation and the present. This result supports the view that neither 6 ka nor the last interglacial provides analogues for the changes in climate and vegetation that are likely to occur in response to rising atmospheric CO_2 concentration (Webb and Wigley, 1985; Gallimore and Kutzbach, 1989; Mitchell, 1990; Crowley, 1993; Rind, 1993). Finally, none of the 'warm climate' scenarios produce a biome response that approaches the magnitude of the difference between the present day and the LGM.

It would be useful to carry out parallel calculations based on a larger sample of palaeoclimate simulations, making use of the standardized 6 ka and LGM results from the Paleoclimate Modeling Intercomparison Project (PMIP) (Harrison et al., in press). Our preliminary comparisons suggest that the projected biome changes due to a doubling of CO_2 are of a magnitude comparable with (although qualitatively different from) the natural, orbitally-induced changes in vegetation that have taken place during the latter half of the Holocene. Based on PMIP results to date (Harrison et al., in press), we suppose that this result will not be radically changed by including other 6 ka simulations. However these natural changes took place

during 6000 years, whereas the predicted future changes are expected to take place almost two orders of magnitude faster (Kattenberg et al., 1996). While climate changes are taking place on the time scale of a century or less, actual vegetation is expected to be very different from potential natural vegetation, due to time lags associated with successional and migrational processes (Pitelka et al., 1997).

Some reasonable criticisms could be made with respect to the way we have employed palaeoclimate simulations. One potential problem is the neglect of biogeophysical feedbacks. We have treated the response of vegetation to climate change as a one-way process, neglecting the fact that major changes in biome distribution are bound to evince further changes in climate. Several recent palaeoclimatic studies have addressed this issue, with a focus on 6 ka. Sensitivity experiments with AGCMs, and experiments with coupled atmosphere-biosphere models, have established that biogeophysical feedbacks could potentially increase the extent of biome boundary shifts between 6 ka and present by at least 50% and in some regions by more than that (e.g. Foley et al., 1994; Kutzbach et al., 1996; Claussen and Gayler, 1997; Texier et al., 1997). The inclusion of such feedbacks has been shown to bring the simulated biome distributions more closely in line with available palaeoecological data (TEMPO, 1996; Texier et al., 1997; Harrison et al., in press). However if such feedbacks were operative at 6 ka they presumably also were operative at other times and should be considered, along with the effects of land-use changes, when projecting climate changes into the future (Melillo et al., 1996). Thus, we suppose that inclusion of feedback effects would potentially increase all of the ΔV values in this paper, but this can only be checked if all of the relevant simulations are carried out using coupled models.

A further possible concern is with the sensitivity of vegetation to CO_2 through physiological (non-climatic) responses by changing stomatal behaviour and the competitive balance between plants expressing the C_3 and C_4 photosynthetic pathways. BIOME 1 does not include such responses. Recent experiments with newer models, such as MAPSS (Neilson, 1995) and BIOME 3 (Haxeltine and Prentice, 1996), suggest that these physiological effects could be important for biome distribution changes both today (VEMAP, 1996) and during the transition between LGM and Holocene (Jolly and Haxeltine, 1997). Such effects should be taken into account by implementing ΔV for a wider range of ecosystem models, and using these models for global impact assessments. By turning on or off the direct CO_2 effects, it would then also be possible to quantify the relative contributions of simulated climate and CO_2 effects.

A wide range of further extensions of the methodology presented in this paper can be imagined. It would be revealing to analyse a wider selection of $2 \times CO_2$ climate model projections with ΔV. It would be instructive to compare ΔV for transient versus equilibrium climate model results, and to follow the temporal evolution of ΔV during transient runs (bearing in mind that ΔV measures potential natural vegetation; actual vegetation would not be expected to track ΔV). ΔV could also be calculated for specific regions; this would undoubtedly reveal greater differ-

ences among models, for example in the response of winter-temperature controlled biome boundaries to CO_2, which differs substantially between the GFDL and OSU simulations (Prentice and Sykes, 1995) and between different palaeoclimate model simulations for 6 ka (Harrison et al., in press).

We conclude with a remark on the design of $\Delta \mathbf{V}$. It may seem surprising to physical or biological scientists that we have included an explicitly subjective element into the design of a dissimilarity measure for analysing the output of natural-science based models. However, we consider this (a) unavoidable, because there is no given scale in which to compare different attributes of vegetation; and (b) desirable, in the sense that it allows alternative implementations to be developed for specific purposes. If we had simply listed a number of attributes and assigned them equal weight, we would merely have concealed the problem: some form of weighting would still have been implicit in our choice of attributes to include or exclude. Alternative implementations, especially for policy-related assessments of climate change 'severity', might for example use subjective weights derived from questionnaire data. In this case the relevant benchmark would not be palaeoclimates but might for example be more recent changes due to non-climatic causes, such as recent landscape transformation by human activities. The extent of such transformation could be estimated by comparing potential natural vegetation maps with actual vegetation estimated by remote sensing.

Thus, we envisage our implementation of $\Delta \mathbf{V}$, and its possible extensions, as tools with a wide range of uses in the contexts of both earth system science and integrated assessment of global change impacts.

Acknowledgements

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