

## Vulnerability of plant communities to breakup under global warming: An index of community integrity

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**Abstract.** Results from recent studies suggest that some familiar plant communities could be vulnerable to significant breakup under global warming, due to different responses of their main defining elements to changing environmental conditions. In order to assess the vulnerability of present-day plant communities to breakup, climatic envelope models were constructed for the main structural elements of some major plant communities (landscapes) of eastern North America, based on the main climatic factors which seem to be best correlated with their current boundaries. Potential changes in species ranges were then studied under plausible global warming scenarios, and an Index of Community Integrity was developed to estimate the changing patterns of community completeness and fitness of the main species. Only very preliminary results are presented here. The question is posed whether such a single-valued integrity index is in fact a useful tool for assessing community integrity and landscape vulnerability under changing environmental conditions.

**Keywords:** Beech-Maple Forest; Community breakup; Eastern North America; Envelope model; *Fagus grandifolia*; Index of Community Integrity; Species fitness; Vulnerability assesment.

### Introduction

During the last Pleistocene glaciation, some plant communities and corresponding landscapes existed in eastern North America which have no present-day analogs, while some important present-day communities either did not exist or were at least not widespread (e.g. Delcourt & Delcourt 1985; Overpeck et al. 1991). The loss during the 20th century of *Castanea dentata* from Appalachian forests shows that, even today, plant communities which we recognize in the landscape may in fact not be entirely stable. Even if no plant community is stable in a strict sense, however, the overlapping ranges of species with similar physiological requirements and often similar physiognomy have resulted in species assemblages which have existed long enough to develop into the ecological and biogeographic units which we recognize today as major communities. Pollen records and other evidence of vegetation redevelopment since the last glaciation suggest that recognizable units similar to most of those of today, such as northern *Fagus-Acer* forest or southern *Quercus-Carya* forest, have existed for many centuries and probably millenia (e.g. Watts 1983).

Under global warming, the geographic ranges of many plant species are expected to shift, generally poleward and upslope. Different tolerance limits, and perhaps changes in the operative limiting factors, will cause co-existing species to respond differently to such changing conditions. If the main structural elements of plant communities do not migrate together, the potential exists for breakup of familiar present-day natural communities over much or even all of their present ranges. Communities do not have to be stable in order to be vulnerable to such breakup, since breakup in this sense represents much greater and faster instability than exists otherwise. Results from a recent study in Florida suggested that some familiar present-day plant communities could be greatly displaced and show significant degrees of area reduction, i.e. breakup, under global average warming of as little as 1 - 2°C (Box et al. 1999).

The possibility of significant community breakup suggests that measures may be needed to estimate the integrity of plant communities and their vulnerability under foreseeable climatic changes. Biological integrity normally implies a degree of wholeness but may also reflect the degree to which processes are functioning normally and main elements are well adapted to environmental conditions ('fitness'). Under global warming, plants will not only shift their locations but will also undergo changes in fitness across their ranges, with different species shifting in different ways. Community wholeness and member fitness may represent the best basis for studying vulnerability, since these concepts, taken together, permit:

- (1) description of the potentially stable core areas of communities, where one may expect them to be best developed (main species most fit);
- (2) identification of more transitional peripheral areas, which may be more vulnerable to perturbations (species less fit, some perhaps missing); and
- (3) identification of environmental gradients which may suggest regions of particular vulnerability under environmental change.

The concept of ecological integrity is not new or old (cf. Frey 1975; Westra 1998). The MFI index (Measured Functional Integrity, cf. Loucks 1998) and IBI (Index of Biological Integrity, cf. Karr 1994) have been actively used in North America for some time. None of the integrity measures which have been presented, however, is designed for predictive use with changing environmental conditions, which may require calibration for large numbers of taxa over large areas. The purpose of this project is thus:

- (1) to define a measure of community integrity based on data which could be readily available for large numbers of species, while still meeting specific ecological criteria; and
- (2) to explore how such a measure may be used and what information it may provide in a particular situation involving a hypothetical but plausible warming scenario.

The region employed is eastern North America, from eastern Canada to central Florida, including the Appalachian Mountains. This paper presents an Index of Community Integrity, some simple results, and explores initially whether such a single-valued integrity index would be a

useful tool in landscape management and vulnerability assessment.

### Data and Methods

The basic methodology involves use of climatic envelopes, i.e.  $n$ -dimensional hyperspaces defined by the putative upper and lower tolerance limits of biological entities relative to sets of climatic variables assumed to represent the main climatic factors limiting their distributions (Box 1981). For plants, the entities can be species, higher taxa, plant functional types or communities (cf. Box 1996, 1987; Box et al. 1993). The main climatic factors and variables which may represent them were discussed by Box (1995). The data required are the geographic ranges of the entities and climatic data from a large number of meteorological stations adequately covering the physiographic heterogeneity of the region of interest. An important shortcoming of envelope models is that envelopes do not include possible metabolic adjustments by plants, such as to higher CO<sub>2</sub> levels and temperatures, which may modify their physiologies and geographic responses to change. There are essentially no data, however, for parameterizing such adjustments, even if their mechanisms were understood (which they are not, for the most part). As a result, in the absence of generally reliable metabolic models, easily calibrated envelope models may still be the only geographically applicable tool for studying possible responses of large numbers of species to climatic changes.

Climatic envelopes are calibrated by iteratively matching range boundaries with the corresponding climatic values and checking the predicted spatial result. Even parameterization based on accurate range maps, however, does not automatically imply reproducibility of the taxon range, since non-climatic factors may also be limiting, at least in some areas. As a result, accurate re-prediction of a taxon range is not circular logic but rather represents confirmation that climate was the overriding control of that range. A study of 120 major woody plant species in Florida confirmed that this climatic approach can capture much of the spatial variability of plant species ranges, even in a region with pervasive control of vegetation patterns by substrate properties and topography (Box et al. 1993).

For the present study, climatic envelopes were constructed and calibrated for over 200 major plant species (mostly woody) of eastern North America, based mainly on range maps by Little (1971, 1977, 1978) but also on other range maps (e.g. Brockman 1984; Jones & Coile 1988; Mellinger 1984; Radford et al. 1968) and previous correlations between vegetation and climate (e.g. Greller 1989; Box et al. 1993). As an example, the climatic envelope of *Fagus grandifolia*, an important canopy co-dominant tree species extending from eastern Canada to northern Florida, is shown in Table 1, along with climatic data suggesting its fitness at Boston (Massachusetts). The 200 species envelopes were then applied to present-day climatic data for about 500 meteorological stations throughout eastern North America and to values (at those sites) representing a hypothetical 2°C global-average warming scenario. This sce-

nario, considered to be realistic for the mid to later 21st century, involves greater warming in winter than in summer and greater warming at higher latitudes and in more continental areas, as suggested by Anon. (1994) and Smith & Tirpak (1989). Under this scenario, winter warming would range from 2–3°C in the southeastern USA to more than 5°C in southern Canada, with summer warming of less than half these amounts.

In order to study the wholeness aspect of community integrity, 15 main plant communities of eastern North America were defined in terms of their main structural elements. This is done at two levels:

(1) those species which are required for community occurrence; and

(2) those additional species which are major, characteristic elements but which do not necessarily occur everywhere the community occurs.

For example, *Fagus grandifolia* and *Acer saccharum* are required for the occurrence of Beech-Maple Forest, but beech may only be an 'additional' or companion species in Northern Mixed Forest, which requires *Pinus strobus* and extends further north than the range of *Fagus*. Such definitions for several major plant communities in eastern North

Table 1. Climatic envelope of *Fagus grandifolia* and application to estimate species fitness at a site.

The potential range of a species can be estimated by its climatic envelope, consisting of its upper and lower tolerance limits relative to its main climatic limiting factors:

	Tmax	Tmin	Tmmin	Tabmin	Mly	Pmin	Defy
Maximum	29.0	13.0	9.0	-7.0	***	***	200.
Minimum	17.0	-12.0	-15.0	-40.0	1.10	40.	0.

Tmax = mean temperature of the warmest month (°C)

Tmin = mean temperature of the coldest month (°C)

Tmmin = mean nighttime minimum temperature of the coldest month (°C)

Tabmin = absolute minimum temperature (°C: coldest ever measured, generally over at least 30 years)

Mly = annual moisture index: precipitation / potential evapotranspiration

Pmin = average precipitation of the driest month (mm)

Defy = annual climatic moisture deficit (mm, as obtained from a climatic water budget)

*Fagus grandifolia*, which occurs from southern Canada to the Gulf of Mexico (western Florida), requires a significant degree of winter cooling (e.g. Tmin < 13°C) but not necessarily continuing periods of sub-freezing temperatures (Tmmin as high as +9°C). It also requires a generally moist climate (Mly at least 1.10—higher than for most oaks, for example), with no extreme dry month (Pmin at least 40 mm), but can tolerate some degree of cumulative moisture stress over a year (Defy up to 200 mm). Limits which are considered unimportant or unattainable are left open-ended and denoted by asterisks. For the significance of these (and other possible) climatic factors in limiting species ranges, see Box (1995, 1996; Box et al. (1993).

Fitness at a site is estimated by applying the climatic envelope to site climatic conditions, for example at Boston:

	Tmax	Tmin	Tmmin	Tabmin	Mly	Pmin	Defy
Boston	21.8	-2.6	-6.7	-27.8	1.70	80	37

Comparison of the Boston site data and the envelope limits of *Fagus grandifolia* shows that it is well within the range for all variables (dimensions) in its climatic envelope. Normalizing for the different range widths (and units) of the different climatic variables suggests that the closest limiting factor is the annual moisture index Mly—although it is still quite far away from that limit. On a 0–1 scale representing the fraction of total normalized width, the proximity to the closest limit is 0.29. This value, called  $d_{min}$ , is used as the estimate of fitness at the site. (For further details see Box 1981, in particular pp. 44–45).

America, with their required and main companion species, are shown in Table 2.

Community integrity, as discussed above and as a predictive tool at particular sites, also requires some measure of the relative fitness of the main structural components. The biological data available at a site are the presence/absence of each species and the proximity of each species to its closest climatic limit, as provided by the climatic envelopes on a normalized 0 - 1 scale (see Table 1). This proximity, denoted  $d_{min}$  in earlier envelope applications (e.g. Box 1981), provides the basis for calculating the index of community integrity.

### An Index of Community Integrity

The Index of Community Integrity (ICI) is estimated entirely from species fitness data (normalized proximity to closest climatic limit), based on the two-level system of required and companion species described above. A community is considered to occur only if all required components are present, but not all companion species are required. Thus, the ICI has two parts:

- (1) a main, multiplicative part based on the fitness of the required species; and
- (2) an additive part based on the fitness of additional, companion species.

This two-part definition is necessary so that multiplication of different numbers of companion fitness values (all < 1) does not bias the result. The fitness values are the proximity scores ( $d_{min}$  values) obtained from application of a full set of species climatic envelopes at a site. Calculation of the ICI is explained in Table 3. The Beech-Maple Forest at Boston (see Table 1) can serve as an example. In that case, the  $d_{min}$  values for both beech and maple were 0.29. Using 0.35 as a good  $d_{max}$  value (see step 3 in Table 3), one gets 0.687 for the base ICI value. There are no companion species (OR species) in the definition of beech-maple forest (see Table 2), so step 4 is not needed in this example and the final ICI value is also 0.687.

The ICI can be summarized by its main properties:

- The ICI is based mainly on the occurrence and fitness of the main species which define the community.
- The ICI varies from 0 to 1, increasing as species fitness increases (i.e. species are farther from climatic limits).
- The ICI is independent of the variables and algorithm used for estimating species fitness; nevertheless, comparison of results from different models requires consistency in variables and algorithms.
- The ICI is based on species which are required (REQ) to define the community and on characteristic companion species, only some alternatives (OR) of which must occur.
- The value of the ICI is not affected by the number of defining species occurring, since absence of any required (REQ) species means that the community does not occur at all.
- The ICI is augmented, at least to some extent, by the most fit defining elements, even if these are companion species which are not required (i.e. not REQ or OR species).

Table 2. Definition of plant communities based on their main defining structural elements.

Beech-Maple Forest		<i>Quercus alba</i>	OR
<i>Acer saccharum</i>	REQ	<i>Carya glabra</i>	
<i>Fagus grandifolia</i>	REQ	Mixed Mesophytic Forest	
Northern Mixed Forest		<i>Fagus grandifolia</i>	REQ
<i>Acer saccharum</i>	REQ	<i>Fraxinus americana</i>	REQ
<i>Pinus strobus</i>	REQ	<i>Liriodendron tulipifera</i>	REQ
<i>Betula lutea</i>	REQ	<i>Acer saccharum</i>	REQ
<i>Fagus grandifolia</i>		<i>Tilia heterophylla</i>	REQ
Piedmont Oak-Hickory Forest		<i>Quercus rubra</i>	OR
<i>Quercus falcata</i>	OR	<i>Quercus alba</i>	OR

Communities are defined by the occurrence of three types of main structural elements: (1) species which must occur (REQ); (2) species in a group of alternatives, only one species of which must occur (OR); (3) other, companion species. Beech-Maple Forest, for example, requires both *Acer saccharum* and *Fagus grandifolia*, and is considered not to occur if either species is absent. Piedmont Oak-Hickory Forest, on the other hand, is considered to occur if either of its two defining *Quercus* elements occurs, since either can be a canopy dominant. Other species (neither REQ nor OR) may also be characteristic of a community and contribute to community integrity by their presence, for example *Fagus grandifolia* in northern mixed forest. Mixed Mesophytic Forest, the most diverse deciduous forest type in eastern North America (windward west side of the central Appalachian Mountains), requires a larger number of defining elements.

- Occurrence of companion species can compensate for lower fitness among the required (REQ and OR) elements — but only to a certain extent (not to exceed ICI = 1.0).
- The value of the ICI is never reduced by the occurrence of additional companion species, since their contributions to the index are added (not multiplied).
- The value of the ICI is 0 if a REQ species or the operative

Table 3. Calculation of the Index of Community Integrity based on proximity to closest envelope limit.

1. Identify the minimum species basis for identifying integrity at the site. This basis must include all REQ and at least one OR species and must involve at least half (and at least two) of all species defining the community. All other defining species which occur at a site are referred to as 'companion' species. If not all required species occur at a site, the community is considered not to occur at that site (i.e. fragments of communities may occur, but only up to a point).
  2. Order all defining species in order of decreasing fitness, as estimated by proximity ( $d_{min}$ ) to the closest environmental limit in an envelope model.
  3. Calculate the normalized product of the fitness value of all species in the minimum basis: Base ICI =  $\pi d_{min}(i) / d_{max}$  ( $\pi$  from  $n$  to  $n_{min}$ ) where the  $d_{min}(i)$  values, for each species  $i$ , come from envelope processing and  $d_{max}$  is a standard value at least as large as the largest  $d_{min}$  to be encountered, and perhaps somewhat larger, in order to normalize for all sites to be processed. (A good  $d_{max}$  value for this purpose seems to be around 0.35, since individual  $d_{min}$  values rarely exceed 0.5 even for widespread, non-defining species such as grasses. If a  $d_{min}$  value exceeds  $d_{max}$  the fraction is truncated at one.)
  4. Beyond the minimum basis (if more species occur), let the "companion" species augment the integrity index as follows. For each additional species:
    - (a) Calculate the remaining integrity deficit, i.e.  $def = 1.0 - ICI$ ;
    - (b) Multiply this remaining deficit by the fitness of the next species  $i$  (arranged in descending order, see item 2 above):  $x_{add}(i) = d_{min}(i) \times def$ ;
    - (c) Add this contribution to reduce the deficit (asymptotically):  $ICI \rightarrow ICI + x_{add}(i)$
- This method has the advantage that ICI can never exceed 1.0 — and cannot even reach 1.0 unless an additional species has a perfect fitness value of  $d_{min}(i) = 1.0$ . Example: For beech-maple forest at Boston (see Table 1), the  $d_{min}$  values for both beech and maple were 0.29; using 0.35 as the  $d_{max}$  value (step 3), the base ICI becomes 0.687. In this case step 4 is not involved, since there are no other defining species for beech-maple forest.

Table 4. Estimated integrity of Beech-Maple Forest at present and under 2°C global average warming.

Location	Lat	Nspp	Integrity Index		
			Now	+2°C	Change
Québec, Québec	46.80	24		.392	.392
Sault Ste. Marie, Michigan	46.47		20	.223	.223
Montréal-Dorval, Québec	45.47	40	.073	.544	.471
Burlington, Vermont	44.47	43	.126	.395	.269
Lake Placid, New York	44.28	15		.180	.180
Concord, New Hampshire	43.20	48	.526	.617	.091
Syracuse, New York	43.12	63	.394	.327	-.068
Buffalo, New York	42.93	65	.510	.360	-.150
Albany, New York	42.75	68	.360	.395	.035
Boston, Massachusetts	42.37	70	.687	.327	-.360
Chicago, Illinois	41.98	71	.160	.138	-.022
Hartford, Connecticut	41.93	76	.687	.340	-.347
Providence, Rhode Island	41.73	77	.687	.286	-.401
Akron, Ohio	40.92	76	.360	.235	-.125
New York, New York	40.78	110	.236	.114	-.122
Pittsburgh, Pennsylvania	40.50	86	.184	.082	-.102
Harrisburg, Pennsylvania	40.22	93	.264	.106	-.158
Columbus, Ohio	40.00	81	.184	.118	-.066
Indianapolis, Indiana	39.73	84	.360	.167	-.193
Baltimore, Maryland	39.28	107	.117		-.117
Washington, D.C.	38.85	103	.099	.022	-.077
Charleston, West Virginia	38.37	105	.264	.046	-.219
Lexington, Kentucky	38.03	102	.236	.064	-.172
Charlottesville, Virginia	38.03	108	.183		-.183
Elk Knob, Virginia	36.87	87	.300	.034	-.266
Boone, North Carolina	36.22	58	.555	.027	-.528
Nashville, Tennessee	36.12	89	.065		-.065
Asheville, North Carolina	35.43	100	.137		-.137

The integrity estimates under current conditions suggest that the core area of beech-maple forest, where it is perhaps best developed and far from climatic limits, is in lower elevations of New England. It may potentially extend, however, with reduced fitness, as far west as Chicago and as far south as the foothills of the southern Appalachians (e.g. Asheville). Under average global warming of 2°C, beech-maple forest could move into more of southern Canada but may retreat entirely from all but higher elevations of the southern Appalachians and from areas as far north as Chesapeake Bay (cf. Baltimore), hanging on only with much reduced fitness in remaining areas of the middle and lower northern Appalachians as well as parts of southern New England. Sites are arranged from north to south by latitude. The second column of numbers (Nspp) shows the number of species predicted to occur at the site, out of the 200 in the envelope model.

OR species has a fitness value of zero (i.e. occurs exactly at a climatic limit) — unless the index is augmented by greater fitness among companion species; ICI = 0 means that the community does occur but is exactly at its limit.

#### Integrity and vulnerability over a range of a communities

In order to assess the usefulness of the Index of Community Integrity, the ICI was calculated for 15 major plant communities across eastern North America, under current climatic conditions and for the 2°C global-average warming scenario described above. The result for beech-maple forest is shown in Table 4. Mapping of such results is being explored and will of course make the results easier to interpret.

The integrity estimates under current conditions suggest that the core area of beech-maple forest should be in lower elevations of New England, where it is indeed best developed, but that it could extend as far west as Chicago and as far south as the foothills of the southern Appalachians. Its main species would have reduced fitness in these peripheral areas, and the community would probably be replaced by forest communities involving species which are more competitive at these locations. Prediction of the range of a community using the ICI thus requires prediction of other possible communities also.

Gradients of community integrity and of vulnerability to warming-induced instability or breakup can be estimated by studying the ICI changes between two scenarios. In Table 4, the column +2°C shows the ICI values for the 2°C global-average warming scenario. The result suggests that Beech-Maple Forest could move into more of southern Canada (where *Acer saccharum* already occurs but not *Fagus grandifolia*) and retreat entirely from all but higher elevations of the southern Appalachians and from lowland areas as far north as Chesapeake Bay. The net effect across eastern North America is a potential loss of area by the Beech-Maple Forest, as suggested by the mostly negative change values in the last column of Table 4. These results are consistent with those for individual species (e.g. Zabinski & Davis 1989), but the ICI provides a quantitative gradient based on the integrated effects of many species.

#### Conclusion

The Index of Community Integrity provides an integrated quantitative estimate of community completeness and fitness, and conversely of community vulnerability to disruption by climatic change, based on:

- (1) present-day correlation between species ranges and climatic conditions; and
- (2) application of such information (as envelope models) to large numbers of sites within and around the ranges of the species involved.

The results not only estimate community 'wholeness' over its range but also the 'fitness' of the main species and their potential for migration based on proximity to climatic limits. The Index of Community Integrity can be based on any reasonable measure of species fitness, but the use of readily calibrated climatic envelope models, based on major climatic constraints, provides a relatively easy means of generating the fitness estimates needed to apply the ICI to large numbers of species over large areas.

Vegetation types whose main structural elements are many or which have wide tolerance limits may be least vulnerable to warming-induced instability or breakup. In the real world, however, vulnerability or at least severe stress may also be affected by geographic 'accidents' such as the shapes of the land masses involved and by factors which we still understand poorly, such as metabolic adaptations and the long-term influence on future vegetation potentials of the transient-state vegetation, which is assumed to be quite weedy.

The results presented here are very preliminary, but the

example of beech-maple forest does illustrate, to some extent, how potentially vulnerable areas may be identified. Whether any such single-valued index provides useful (and not misleading or artificial) information for natural-area and landscape management, however, may still be an open question.

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