Ecological Risk–Benefit Analysis of a Wetland Development Based on Risk Assessment Using “Expected Loss of Biodiversity”

Toshihiro Oka,1,2* Hiroyuki Matsuda,2,3 and Yasuro Kadono4

Ecological risk from the development of a wetland is assessed quantitatively by means of a new risk measure, expected loss of biodiversity (ELB). ELB is defined as the weighted sum of the increments in the probabilities of extinction of the species living in the wetland due to its loss. The weighting for a particular species is calculated according to the length of the branch on the phylogenetic tree that will be lost if the species becomes extinct. The length of the branch on the phylogenetic tree is regarded as reflecting the extent of contribution of the species to the taxonomic diversity of the world of living things. The increments in the probabilities of extinction are calculated by a simulation used for making the Red List for vascular plants in Japan. The resulting ELB for the loss of Nakaikemi wetland is 9,200 years. This result is combined with the economic costs for conservation of the wetland to produce a value for the indicator of the “cost per unit of biodiversity saved.” Depending on the scenario, the value is 13,000 yen per year-ELB or 110,000 to 420,000 yen per year-ELB (1 US dollar = 110 yen in 1999).

KEY WORDS: Probability of extinction; taxonomic diversity; risk–benefit analysis; wetland; ecological risk

1. INTRODUCTION

Quantitative risk assessment has been well established, as far as adverse effects of environmental pollution on human health are concerned; and risk management based on quantitative risk assessment is becoming more widely used in policy making.1,2 Quantitative risk assessment is also needed for determining the ecological effects of environmental degradation to ensure that the management of the ecosystem is based on rational grounds. In this article, a new method of assessing the ecological risk by using the index of “expected loss of biodiversity” (ELB) is presented. ELB is defined as the weighted sum of the increments in the probabilities of extinction of species that would be caused by human activities such as land-use conversion or pollution. The weighting for a particular species is assigned a value equivalent to the length of the branch on the phylogenetic tree that will be lost if the species becomes extinct. We applied this method to a case of land-use conversion in Nakaikemi Wetland, Japan. The result was combined with the economic benefits from the development of the wetland, to produce an indicator of cost effectiveness—that is, “cost per ELB” of the conservation of the wetland.

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We developed the measure, ELB, to fulfill the need for expanding the framework of risk assessment from human health risks to ecological risks. One reason why ecological risk assessment is not as established as human health risk assessment is that an appropriate end point has not been determined. In human health risk assessment, “death” of individual human beings is most widely adopted as the end point for risk assessment, and risk is expressed in terms of the probability of death or of the indicator closely linked with the probability of death, such as loss of life expectancy. As Nakanishi\(^{(3,4)}\) pointed out, the success of health risk assessment is indebted to the fact that the end point is an event that everyone wants to avoid. On the contrary, in ecological risk assessment, various endpoints are adopted, most of which are not unanimously agreed on. For instance, one may accept the death of some individuals of a particular animal species, or one may even accept the loss of a habitat of several plant species. Nakanishi suggested adopting the extinction of species as the end point for ecological risk assessment, in that extinction must surely be an event that everyone wants to prevent. The present study is an attempt to actualize this proposal.

ELB is also a measure to link conservation of local ecosystems with global biodiversity. Conservation of local ecosystems has been treated as an issue separate from conservation of global biodiversity. It is certainly easy to envisage that the existence of local ecosystems contributes to global biodiversity, but it has been the intrinsic values of local ecosystems that have advanced the local ecosystems’ conservation. When the biodiversity of local ecosystems is considered, it is often measured by an indicator that can be defined within the ecosystem independently from the world outside.

There are several indices for species diversity in community ecology. Species richness is defined as the number of observed species. Two other measures of species diversity, Shannon’s index and Simpson’s index, include relative abundance of each species. Shannon’s and Simpson’s indices are respectively defined as \(\sum_i - P_i \log P_i\) and \(\frac{1}{\sum_i P_i^2}\), where \(P_i\) is the relative abundance of species \(i\). Contribution of rare species on these indices is very small. Loss of rare species with decrease of other species slightly decreases or sometimes increases these indices. Therefore, conservation ecology usually uses species richness as an appropriate index of species diversity. This index, however, can be defined independently from the world outside of the land. The present study is an attempt to combine the issue of local ecosystems with that of global biodiversity. We developed a measure for the contribution of a particular local ecosystem to global biodiversity.

2. NAKAIKEMI WETLAND

The case to which we attempted to apply our method of ecological risk assessment is the development of Nakaikemi Wetland. Nakaikemi Wetland (Tsuruga, Japan) is a wetland of about 25 ha, which is characterized by the presence of exceedingly deep peat sediments (ca. 50 m in depth), which contain records of paleoenvironmental changes during the past 50 thousand years. Most of the area has been used as rice paddy for hundreds of years, but recently more than two thirds of the land lies fallow according to a set-aside policy, because this area has a low rice-growing productivity. Abandoned rice fields have been found to support a remarkable biodiversity.\(^{(5)}\)

The area supports many species of aquatic plants that are regarded as declining nationwide, including 13 of the “threatened” and 2 of the “near-threatened” (NT) plant species according to the Red List published by the Japanese Environment Agency in 1997.\(^{(6)}\) There are also many species of fish, including threatened cyprinodont, and insects, including more than 60 kinds of dragonflies and several kinds of diving beetles.

In 1992, Osaka Gas Company (OGC) planned the construction of a liquefied natural gas (LNG) plant in this area. The procedure for the environmental impact assessment was completed in 1996, whereby the government of Fukui Prefecture approved the OGC plan on condition that the company transplant all the rare and threatened plant species to an area of 3.3 ha within Nakaikemi, which is called the “protected conservation area,” and that a transplantation test be conducted for 3 years. A protection movement opposed to the development plan was organized as soon as the plan was made public. The Ecological Society of Japan issued a statement calling for the preservation of the entire wetland in 1996.

OGC argues that the natural life on this wetland is secondary; that is, created as a by-product of human cultivation, and that the protection of the plants in the conservation area is sufficient to maintain the biodiversity of this land, although the conservation area is much smaller than the entire wetland. Ecologists oppose this argument by asserting that the trans-
plant will not succeed owing to the complexity of the relation among the species living in the wetland; that no one can judge the success of the transplant in 3 years; and that human-controlled nature in such a small area is not the same as what existed before and, therefore, the whole area should be conserved with the traditional utilization of the land as a rice field.

3. FRAMEWORK

Our framework for combining a local ecosystem with global biodiversity and for expressing the risk from the loss of a local ecosystem in terms of probability of extinction is as follows:

1. Loss of a local ecosystem means loss of one habitat of the species living there. This loss would, thereby, raise the probability of the species' nationwide extinction.
2. Extinction of species would reduce global biodiversity. The impact is measured by the species' contribution to global biodiversity.
3. The sum of the increments in the extinction probability weighted by the contribution to biodiversity for all the species living on the land can be called the ELB. The ELB for the development of Nakaikemi was estimated.

4. INCREASES IN THE PROBABILITY OF EXTINCTION

4.1. Method

Our estimate of the increases in the extinction probabilities was based on the simulation used in making the Red List for vascular plants in Japan. The Red List was created in 1997, following the categories and the criteria of the IUCN (The World Conservation Union) Red List of 1994 and adopted the quantitative assessment of the probabilities of extinction for each of the vascular plants. Among the five criteria, the so-called criterion “E” is based on the quantitative assessment of the extinction probability. This criterion classifies the threatened species as

- critically endangered (CR), if the probability of extinction is larger than or equal to 50% in 10 years or three generations;
- endangered (EN), if the probability of extinction is larger than or equal to 20% in 20 years or five generations; and
- vulnerable (VU), if the probability of extinction is larger than or equal to 10% in 100 years.

Actual classification was made according to the criterion that gave the most severe result among the so-called criterion “ACD” and the criterion E.

The assessment of the extinction probabilities was made by a simulation based on the data on the number of sites in which a species exists, the population size at each site, and the nationwide distribution of the reduction rates of the population in the past 10 years. The data were collected from about 400 researchers. The simulation assumed the distribution of the reduction rate in the past 10 years would hold in the future, and conducted 1,000 trials to assess how many times a species would become extinct within the next 100 years.

This simulation produces the mean time for the extinction of each species $T$. By using this simulation, we can also calculate the mean time for extinction when one of the habitats is lost. Ordinarily, the time for extinction would be reduced when a habitat is lost, and the larger the population size on the habitat, the larger the reduction would be. Therefore, this reduction in the time for extinction ($\Delta T$) is regarded as representing the impact of the loss.

The reciprocal of the mean time for extinction is interpreted as representing the probability of extinction per year, if extinction in each year can be regarded as occurring independently from extinction in other years. We adopted the increment in the reciprocal of the mean time for extinction, namely $\Delta(1/T)$, as an indicator for the impact of a habitat loss on the nationwide extinction of a species.

The assumption of independence of extinction is restrictive, taking into consideration the fact that the simulation itself is based on the dependence of extinction in any given year on the decreases in population size occurring in the previous years. However, the change in the time for extinction itself, $\Delta T$, cannot be regarded as representing appropriately the impact of the loss of a habitat. For example, a 1-year decrease from 10 years of survival expectancy should not be the same as a 1-year decrease from 100 years of expectancy, and the impact of the latter should be regarded as smaller than that of the
former. To adopt $1/T$ as a risk measure is one way to deal with this problem.\(^6\)

4.2. Application to Nakaikemi Wetland

There are hundreds of species of vascular plants at Nakaikemi Wetland, but to assess the increments in the extinction rates due to the loss of this land for all species is impossible because the data necessary for making the Red List were not collected for the species that were evidently not threatened. In fact, it is not necessary to assess the impact for all the existing species, because the impact on the extinction probability for the species that are secure must be negligible. Accordingly, we made calculations only for the species included in the categories of “threatened” (consisting of CR, EN, and VU) or of NT species.

For this calculation, it was necessary to know the number of habitats by population size and the number of habitats by rate of population decline. These figures were available from Kankyotyo.\(^6\) Information on the population of each species at Nakaikemi

\(^6\) An alternative approach is to adopt the loss in “discounted years of existence” as a risk measure. If the discount rate is \(r\), the discounted years of existence of a species from year 0 to \(t\) is

$$\int_0^t e^{-rs} dt = \frac{1 - e^{-rt}}{r}.$$  

Because the probability of extinction at year \(t\) is

$$m(t) \exp \left[ -\int_0^t m(s) ds \right],$$

where \(m(t)\) is the probability of extinction within year \(t\), on condition that the species exists until year \(t - 1\), the expected value of the discounted years of existence is

$$L = \frac{1}{r} \int_0^T m(t) \exp \left[ -\int_0^t m(s) ds \right] (1 - e^{-rt}) dt.$$  

When the extinction in each year is independent and \(m(t)\) is constant at \(m\), \(L\) is equal to \(1/(m + r)\). When the probabilities of extinction until year \(T - 1\) are zero and that for the year \(T\) is one, \(L\) becomes \((1 - e^{-r}))r\). The advantage of the expected discounted years of existence is that it allows the dependence of the extinction probabilities. Its disadvantage is that it requires specifying the discount rate. Because the discount rate in the above equations has no relation to that in the economic sense—namely, the people’s rate of time preference, which can be observed in the market place—we have no empirical grounds to determine it. The advantage of \(\Delta(1/T)\) is its simplicity and the fact that it does not need any discount rates. Nevertheless, it requires an implausible assumption that the extinction in each year occurs independently from others in order to allow for the interpretation that it represents the extinction probability per year. However, the measure \(\Delta(1/T)\) is convenient in that we can use the term ELB for the product of the probability of extinction and the species’ contribution to biodiversity.

5. CONTRIBUTIONS TO BIODIVERSITY

5.1. Method

Biodiversity is a broad concept that can contain hierarchical definitions of various levels. It is said to be defined at the level of gene, species, ecosystem, and landscape.\(^10\) The diversity of an ecosystem or landscape is, however, elusive and has to be further refined for operational measurement. Here, we adopt the biodiversity of species as a first approximation. How do we measure the diversity of species? It is said that because the existing diversity of species is the product of the accumulation of speciations having taken place for a very long time, and a speciation, in turn, is a process of trial and error of natural genetic recombinations taking millions of years, the loss of a species is equivalent to the loss of a cultural heritage of tens of millions of years.\(^10\)

The phylogenetic tree can be regarded as a record of the history of speciations. Therefore, the idea of developing an indicator of biodiversity by means of phylogenetic information is quite understandable. The first attempt was made by Vane-Wright, Humphries, and Williams.\(^11\) They regarded the reciprocal of the number of nodes between a particular taxon and the root of the phylogenetic tree as representing the contribution of the taxon to global biodiversity. In the tree shown in Fig. 1, if the contribution to the diversity of sharks is 1, then that of salmon is 1/2, that of frogs is 1/4, and that of kangaroos or antelopes is 1/7. The nearer to the root, the larger the contribution to diversity of a taxon. This approach was later called “root-weighting.”

Vane-Wright et al.,\(^11\) however, were not satisfied with this measure, because it is flawed when
used for “unresolved trees.” In the tree shown in Fig. 2, for instance, every taxon has an equal weight in the root-weighting method, but if two taxa should be chosen, one should be chosen from A or B and the other from C, D, or E in order to conserve more diversity. (12)

Attributing this flaw to the weighting of individual taxa, Williams et al. (12) pursued methods using pairwise measurement of the relative divergence between two taxa. They presented four kinds of pairwise measures using the number of shared nodes between two taxa \( S_{ij} \) for taxa \( i \) and \( j \) and the number of unique nodes for a taxon \( i \) with respect to another taxon \( j \) \( (U_{ij}) \). By using these measures, they developed a criterion of taxonomic dispersion.

The first pairwise measure is \( S_{ij} \), the reciprocal of the number of nodes between a particular taxon and the root of the phylogenetic tree is regarded as representing the contribution of the taxon to global biodiversity. If the contribution to the diversity of sharks is 1, then that of salmon is 1/2, that of frogs is 1/4, and that of kangaroos or antelopes is 1/7. (11)

\[
\Delta(1/T) = \frac{S_{ij}}{S_{ij} + U_{ij}}
\]

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\]

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\]

Table 1. Increments in the Extinction Probabilities of Vascular Plants Due to the Loss of Nakaikemi

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Red List category</th>
<th>No. of habitats</th>
<th>Population at Nakaikemi*</th>
<th>Before the loss (year)</th>
<th>After the loss (year)</th>
<th>( \Delta(1/T) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isoetes japonica</td>
<td>Isoetaceae</td>
<td>VU</td>
<td>149</td>
<td>10–100</td>
<td>89.96</td>
<td>89.89</td>
<td>( 8.9 \times 10^{-4} )</td>
</tr>
<tr>
<td>Marsilea quadrifolia</td>
<td>Marsiliaceae</td>
<td>VU</td>
<td>51</td>
<td>10–100</td>
<td>32.32</td>
<td>32.26</td>
<td>( 6.4 \times 10^{-4} )</td>
</tr>
<tr>
<td>Salvinia natans</td>
<td>Salviniacae</td>
<td>VU</td>
<td>104</td>
<td>10–100</td>
<td>54.57</td>
<td>54.56</td>
<td>( 5.7 \times 10^{-4} )</td>
</tr>
<tr>
<td>Azolla japonica</td>
<td>Azollaceae</td>
<td>VU</td>
<td>80</td>
<td>100–1,000</td>
<td>52.76</td>
<td>52.65</td>
<td>( 4.1 \times 10^{-4} )</td>
</tr>
<tr>
<td>Persicaria foliosa</td>
<td>Polygonaceae</td>
<td>VU</td>
<td>33</td>
<td>1–10</td>
<td>54.00</td>
<td>53.87</td>
<td>( 4.3 \times 10^{-4} )</td>
</tr>
<tr>
<td>Trapa incisa</td>
<td>Trapaceae</td>
<td>VU</td>
<td>50</td>
<td>100–1,000</td>
<td>85.08</td>
<td>84.06</td>
<td>( 1.4 \times 10^{-4} )</td>
</tr>
<tr>
<td>Eusteralis yatabeana</td>
<td>Lamiaceae</td>
<td>VU</td>
<td>17</td>
<td>100–1,000</td>
<td>35.99</td>
<td>35.54</td>
<td>( 3.6 \times 10^{-4} )</td>
</tr>
<tr>
<td>Prenanthes tanakae</td>
<td>Asteraceae</td>
<td>VU</td>
<td>98</td>
<td>100–1,000</td>
<td>119.59</td>
<td>118.87</td>
<td>( 5.1 \times 10^{-4} )</td>
</tr>
<tr>
<td>Sagittaria aginashi</td>
<td>Alismataceae</td>
<td>NT</td>
<td>128</td>
<td>10–100</td>
<td>162.02</td>
<td>161.91</td>
<td>( 4.4 \times 10^{-4} )</td>
</tr>
<tr>
<td>Najas japonica</td>
<td>Najadaceae</td>
<td>EN</td>
<td>29</td>
<td>10–100</td>
<td>37.73</td>
<td>37.51</td>
<td>( 1.5 \times 10^{-4} )</td>
</tr>
<tr>
<td>Monochoria korsakowii</td>
<td>Pontedariaceae</td>
<td>VU</td>
<td>52</td>
<td>10–100</td>
<td>56.44</td>
<td>56.23</td>
<td>( 6.7 \times 10^{-4} )</td>
</tr>
<tr>
<td>Iris laevigata</td>
<td>Iridaceae</td>
<td>VU</td>
<td>81</td>
<td>10–100</td>
<td>102.22</td>
<td>102.15</td>
<td>( 6.3 \times 10^{-4} )</td>
</tr>
<tr>
<td>Sparganium erectum</td>
<td>Sparganiaceae</td>
<td>NT</td>
<td>148</td>
<td>10–100</td>
<td>185.15</td>
<td>185.08</td>
<td>( 1.9 \times 10^{-4} )</td>
</tr>
<tr>
<td>Sparganium japonica</td>
<td>Sparganiaceae</td>
<td>NT</td>
<td>114</td>
<td>100–1,000</td>
<td>202.22</td>
<td>201.77</td>
<td>( 1.1 \times 10^{-4} )</td>
</tr>
<tr>
<td>Habenaria sagittifera</td>
<td>Orchidaceae</td>
<td>VU</td>
<td>121</td>
<td>1–10</td>
<td>81.80</td>
<td>81.79</td>
<td>( 1.5 \times 10^{-4} )</td>
</tr>
</tbody>
</table>

Note: VU = vulnerable; NT = near threatened; EN = endangered.
*Data from Kadono.

Fig. 1. Contribution of taxa to diversity: root-weighting. The reciprocal of the number of nodes between a particular taxon and the root of the phylogenetic tree is regarded as representing the contribution of the taxon to global biodiversity. If the contribution to the diversity of sharks is 1, then that of salmon is 1/2, that of frogs is 1/4, and that of kangaroos or antelopes is 1/7. (11)

Fig. 2. Root-weighting in an unresolved tree. Every taxon has an equal weight in the root-weighting method, but if two taxa should be chosen, one should be chosen from A or B and the other from C, D, or E in order to conserve more diversity. (12)
The dispersion criterion proposed by Williams et al.\textsuperscript{(12)} is

\[
\text{number of spp.} \times \frac{1}{\text{mean divergence}} \left( U_{ij} + U_{ji} + 1 \right) - \text{SD of divergences}.
\]

Under this dispersion criterion, the selection of shark, frog, and [kangaroo or antelope] has the largest diversity. They applied the last criterion to setting priority on the habitats of bumble bees (the siblicias group of \textit{Bombus}) in the world.\textsuperscript{(12,13)}

Weitzman\textsuperscript{(14)} revealed that any measure of diversity based on ultrametric distance can be represented by the length of the branches of a phylogenetic tree. Ultrametric means that the distance between a terminal node and the root node is equal for every terminal. He investigated under what conditions a nonultrametric distance can generate a measure of diversity having desirable properties. The total diversity of a group of species is represented by the total length of the branches of the taxonomic tree for the group, and the distance between any two species in the tree is depicted as the length of the branch between either of them and the node of their nearest common ancestor. The loss of diversity when a species becomes extinct is also represented by the length of the branch between the terminal node of the species and the node of its nearest ancestor that is shared with another species.

For instance, in the tree presented in Fig. 3, taxon A contributes to global diversity by the length of the branch between the terminal node for A and the node representing the nearest common ancestor to A and other taxa, namely \( l_A \). Similarly, taxon F contributes to global diversity by \( l_F \). Accordingly, when they become extinct, the loss of diversity is also \( l_A \) for A and \( l_F \) for F, respectively.

In this framework, the contribution to diversity of a particular taxon is independent from the scope for which total diversity is considered. The diversity of an upper taxon consisting of A and B, for example, is measured as \( l_A + l_B \), to which A contributes by \( l_A \). The diversity of a still upper taxon consisting of A, B, and C is \( l_A + l_B + l_{AB} + l_C \), to which A contributes again by \( l_A \). The loss of diversity due to the extinction of A is, therefore, always \( l_A \), irrespective of the upper taxon for which total diversity is calculated. Extinction of other taxa, however, affects the contribution to diversity of a particular taxon. When B is extinct, for example, A’s contribution will increase to \( l_A + l_{AB} \).

Weitzman\textsuperscript{(15)} applied this measure to setting priority on the protection of the crane species of the world.

The above proposals for the measure of biodiversity by Williams \textit{et al.}\textsuperscript{(12)} and Weitzman\textsuperscript{(14)} are helpful. Unfortunately, they could not be used directly in our attempt to construct a measure of biodiversity that can be used for assessing the contribution of a particular area, such as Nakaikemi Wetland, because of a prohibitive amount of calculation that is necessary for the pairwise measures proposed by Williams \textit{et al.} on the one hand, and a lack of knowledge about branch lengths that is necessary for Weitzman’s measure.

First, any pairwise measures of divergence between species are not suitable for our study. The pairwise measures make sense only when the whole cladogram for all the clades including relevant species is available. Williams \textit{et al.}\textsuperscript{(12,13)} could use their pairwise measure because they had to obtain the values of their pairwise measures for only 43 species within \textit{Bombus}. One can calculate the decrease in the value of dispersion constructed of pairwise measures of divergence due to a loss of some species among those 43 species in one genus.

Nakaikemi has hundreds of animal and plant species, which belong to various genera, families, orders, and so forth. For example, to assess the impact of the extinction of \textit{Iris laevigata}, which lives in Nakaikemi, by using Williams \textit{et al.}’s approach\textsuperscript{(12)} one would have to calculate the dispersion for the cladogram of the genus \textit{Iris} for the case in which \textit{Iris laevigata} exists and for the case in which it does not exist. To take the genus as a clade for which the dispersion is calculated is, however, arbitrary. One could take the family Iridaceae. Because the genus \textit{Iris} has about 200 species, whereas the family Iridaceae has about 1,400 species, the dispersion becomes larger for the family than for the genus because of the large number of

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{fig3.png}
\caption{Weitzman’s measure of diversity. Taxon A contributes to global diversity by the length of the branch between the terminal node for A and the node representing the nearest common ancestor to A and other taxa, namely \( l_A \). Similarly, taxon F contributes to global diversity by \( l_F \). The loss of diversity due to the extinction of A is \( l_A \). When B is extinct, A’s contribution will increase to \( l_A + l_{AB} \).}
\end{figure}
species contained, and, hence, the decrease in the value of dispersion due to the loss of a species would be larger for the family. Furthermore, Nakaikemi has species belonging to other taxa, for example, some species belonging to the genus *Sparganium*, which, in turn, belongs to the family Sparganiaceae. There is no reason, therefore, to reject taking an upper clade including both Iridaceae and Sparganiaceae as, for example, the monocotyledon. Considering the fact that Nakaikemi has flowering plants other than monocotyledons, seed plants other than flowering plants, and vascular plants other than seed plants, the only clade without arbitrariness for which the dispersion is calculated is the highest clade that includes all the species. To calculate the dispersion for the highest clade for all the species is, evidently, impossible.

Weitzman’s approach\(^{(14)}\) is free from this problem, because it can calculate the loss of diversity due to the extinction of some species independently from the choice of the clade for which total diversity is considered. This approach, however, has problems when it is to be used for assessing the diversity contribution of a particular area; that is, it is necessary to know the length of branches in the phylogenetic tree. Weitzman\(^{(15)}\) was able to determine the length of the branches in the phylogenetic tree for 15 crane species by using the genetic distances among them estimated by DNA–DNA hybridization. Nowadays, the method of comparing DNA sequences is widely used to estimate phylogenetic relations. However, genetic distances are not always obtained in such estimation.

Considering these difficulties and the necessity to obtain a diversity measure for a particular area, we proposed to adopt the Vane-Wright et al.’s\(^{(15)}\) original root weighting but to interpret the reciprocal of the number of nodes between the root and the terminal as a surrogate for the length of the branch between the terminal node and the node of the nearest common ancestor with another species, assuming all the branches represent ultrametric distances.

In Fig. 4, \(l_i (i = A, B, C, D)\) represents the length of the branch between the terminal node for species \(i\) and the nearest node shared with another species. The length of the branch between the nearest shared node for \(C\) and \(D\) and the nearest shared node among \(B, C,\) and \(D\) is represented by \(l_{CD}\), and the branch length between the latter node and the nearest shared node among \(A, B, C,\) and \(D\) is represented by \(l_{BCD}\).

In addition to the problem of the lack of knowledge about the real length of branches, there is another problem—that is, a fully resolved phylogenetic tree is not always available. For some families, relations between genera have been well studied, whereas for other families, they have not. In addition, for some genera, relations between species have been well studied, whereas for other genera, they have not. Confronted with this problem, we adopted the approach of using a phylogenetic tree from the root to a certain upper taxon including the species in question, and to estimate the expected value of the reciprocal of the number of nodes between the terminal node for the species and the root from the number of species included in that upper taxon.

For example, when there are four species within an upper taxon, 15 phylogenetic trees can occur within the upper taxon. In three cases, a species, say A, has one node between the root of the upper taxon and itself; in six cases, A has two nodes between the root and itself; and in the other six cases, it has three nodes. Hence, when the upper taxon itself has \(m\) nodes between itself and the root of the whole tree (Fig. 5), the expected mean value of the reciprocal of the number of nodes between the terminal node for species \(A\) and the root of the whole tree is

\[
\frac{3}{15} \times \frac{1}{m+1} + \frac{6}{15} \times \frac{1}{m+2} + \frac{6}{15} \times \frac{1}{m+3}.
\]

When there are \(n\) species within an upper taxon, the number of phylogenetic trees in which a species \(A\) has \(k\) nodes between itself and the root of the upper taxon is

\[
\frac{3}{15} \times \frac{1}{m+1} + \frac{6}{15} \times \frac{1}{m+2} + \frac{6}{15} \times \frac{1}{m+3}.
\]
taxon is represented by \( f_k(n) \) that is represented by the equations

\[
\begin{align*}
    f_1(n) &= f(n-1) \\
    f_k(n) &= \sum_{i=1}^{n-k} C_i f(i) f_{k-1}(n-i), \quad k = 2, 3, \ldots, n-1,
\end{align*}
\]

where \( C_i \) is the combinations of \( n \) things taken \( i \) at a time, and \( f(n) \) represents the total number of phyllogenetic trees when there are \( n \) species, that is,

\[
f(n) = \sum_{i=1}^{n-1} f_i(n).
\]

The expected mean value of the reciprocal of the number of nodes between the terminal node for species A and the root of the whole tree is, therefore,

\[
E_n\left[\frac{1}{m+k}\right] = \frac{1}{f(n)} \sum_{k=1}^{n-1} \frac{f_k(n)}{m+k},
\]

where \( m \) is the number of nodes between the upper taxon and the root of the whole tree.

To obtain the value of \( E_n[1/(m+k)] \) using these equations requires a huge number of calculations when \( n \) is large. Hence, in practice, when \( n \) is larger than 100, we used as an approximation for \( E_n[1/(m+k)] \)

\[
\frac{1}{m + E_n[1/k]},
\]

where \( E_n[1/k] \) is equal to \( E_n[1/k](2n-4)/(2n-3) \).

Any group of taxa can be chosen as the upper taxon, whether a family, a group consisting of two families, or an order or a higher taxon, as long as the taxon is monophyletic. Our interpretation of the root weighting is effective in overcoming the flaw concerning an unresolved tree pointed out by Williams et al. (12). Among C, D, and E in Fig. 2, there are only three possible relations shown in Fig. 6. Because C’s diversity contribution is 1/2 with the probability of 1/3, and 1/3 with the probability of 2/3, the expected value of C’s contribution equals 7/18. Similarly, the contribution to diversity of D or E is also 7/18, whereas the diversity contribution of A or B is 1/2. Therefore, when it is necessary to choose one species to become extinct, that species should be chosen from among C, D, and E. After choosing one, say C, the diversity contribution of D and E increases to 1/2. As a result, if a second species should be chosen to become extinct, all the remaining species will have the same value. Suppose D is chosen; then the diversity contribution of E increases to 1. Therefore, if a third species has to be chosen to become extinct, A or B should be chosen. Consequently, one species will successfully be selected from A and B and one from C, D, and E when two species are required to be preserved among the five in Fig. 2.

5.2. Application to Nakaikemi Wetland

The diversity contribution of the species listed in Table I was calculated according to the approach discussed in Section 5.1. For the relations among Psilotopsida, Lycopodiopsida, Equisetopsida, Polypodiopsida, and Spermatopsida, the tree shown in Fig. 7
Table II. Contribution to Biodiversity and Expected Loss of Biodiversity (ELB) of the Plant Species in Nakaikemi

<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>Upper taxon</th>
<th>No. of nodes above the upper taxon</th>
<th>No. of species within the upper taxon</th>
<th>Contribution to biodiversity&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Y (year)</th>
<th>ELB ∆P/Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Isoetes japonica</td>
<td>Isoetaceae</td>
<td>3</td>
<td>68</td>
<td>0.073</td>
<td>2.9 × 10^7</td>
<td>260</td>
</tr>
<tr>
<td>2</td>
<td>Marsilea quadrifolia</td>
<td>Marsiliaceae</td>
<td>9</td>
<td>67</td>
<td>0.049</td>
<td>2.0 × 10^7</td>
<td>1300</td>
</tr>
<tr>
<td>3</td>
<td>Salvinia natans</td>
<td>Salvinia</td>
<td>10</td>
<td>10</td>
<td>0.071</td>
<td>2.8 × 10^7</td>
<td>160</td>
</tr>
<tr>
<td>4</td>
<td>Azolla japonica</td>
<td>Azollaceae</td>
<td>10</td>
<td>6</td>
<td>0.077</td>
<td>3.1 × 10^7</td>
<td>1300</td>
</tr>
<tr>
<td>5</td>
<td>Persicaria foliosa</td>
<td>Polygonaceae</td>
<td>20–21</td>
<td>1,000</td>
<td>0.018</td>
<td>7.1 × 10^6</td>
<td>300</td>
</tr>
<tr>
<td>6</td>
<td>Trapa incisa</td>
<td>Trapaceae</td>
<td>25–29</td>
<td>15</td>
<td>0.031</td>
<td>1.2 × 10^7</td>
<td>1800</td>
</tr>
<tr>
<td>7</td>
<td>Eusteralis yatabeana</td>
<td>Lamiaceae + Verbenaceae</td>
<td>29–35</td>
<td>580</td>
<td>0.0085</td>
<td>3.4 × 10^6</td>
<td>1200</td>
</tr>
<tr>
<td>8</td>
<td>Preanthus tanakae</td>
<td>Asteraeae</td>
<td>28–29</td>
<td>20,000</td>
<td>0.0053</td>
<td>2.1 × 10^6</td>
<td>110</td>
</tr>
<tr>
<td>9</td>
<td>Sagittaria aginashi</td>
<td>Alismatales</td>
<td>17–19</td>
<td>249</td>
<td>0.028</td>
<td>1.1 × 10^7</td>
<td>49</td>
</tr>
<tr>
<td>10</td>
<td>Najas japonica</td>
<td>Najadales</td>
<td>17–19</td>
<td>205</td>
<td>0.029</td>
<td>1.2 × 10^7</td>
<td>1800</td>
</tr>
<tr>
<td>11</td>
<td>Monochoria korsakowit</td>
<td>Pontedariae</td>
<td>22–26</td>
<td>34</td>
<td>0.030</td>
<td>1.2 × 10^7</td>
<td>800</td>
</tr>
<tr>
<td>12</td>
<td>Iris laevigata</td>
<td>Iridaceae</td>
<td>18–23</td>
<td>1,400</td>
<td>0.016</td>
<td>6.3 × 10^6</td>
<td>40</td>
</tr>
<tr>
<td>13</td>
<td>Sparganium erectum</td>
<td>Sparganaceae</td>
<td>22–27</td>
<td>20</td>
<td>0.031</td>
<td>1.3 × 10^7</td>
<td>24</td>
</tr>
<tr>
<td>14</td>
<td>Sparganium japonica</td>
<td>Sparganaceae</td>
<td>22–27</td>
<td>20</td>
<td>0.031</td>
<td>1.2 × 10^7</td>
<td>140</td>
</tr>
<tr>
<td>15</td>
<td>Habenaria sagittifera</td>
<td>Orchids</td>
<td>17–21</td>
<td>20,115</td>
<td>0.0056</td>
<td>2.2 × 10^6</td>
<td>3.3</td>
</tr>
</tbody>
</table>

Total: 9,200

<sup>a</sup> B<sub>i</sub> is the expected value for the reciprocal of the number of nodes between the terminal node for species <i>i</i> and the root node of the vascular plants, and Y<sub>i</sub> is equal to Bi multiplied by 4 × 10<sup>3</sup>, on the basis of the assumption that the first diversion of vascular plants occurred 400 million years ago.

For the true ferns, the number of nodes above the families was determined according to the molecular phylogenetic tree from Hasebe et al.<sup>19</sup> The nodes for the seed plants were counted according to the phylogenetic tree presented by Chase et al.<sup>20</sup> (B series of their figures).<sup>7</sup>

Families were chosen as the upper taxa and the nodes between them and the root of the whole tree were counted for the vascular plants, except for <i>Eusteralis yatabeana</i>, <i>Sagittaria aginashi</i>, <i>Najas japonica</i>, and <i>Habenaria sagittifera</i>. For these four species, higher taxa were chosen, as shown in Table II. (As for the reason why these taxa were chosen as the upper taxa, see the Appendix discussed in footnote 7.) The result-

was assumed.<sup>16,17</sup> The relation among the three families of Lycopodioptida, namely Isoetaceae, Lycopodiaceae, and Selaginellaceae, is based on the molecular analysis by Manhart,<sup>18</sup> although the molecular analysis has not produced stable results for this level of taxa. As a result, the number of nodes for Isoetaceae between the terminal and the root is three, which is shown in the column. Number of nodes above the upper taxon, for <i>Isoetes japonica</i> in Table II.

For the true ferns, the number of nodes above the families was determined according to the molecular phylogenetic tree from Hasebe et al.<sup>19</sup> The nodes for the seed plants were counted according to the phylogenetic tree presented by Chase et al.<sup>20</sup> (B series of their figures).<sup>7</sup>

For details about the phylogenetic trees and node counting for the true ferns and the seed plants, see the Appendix, which is available via the Internet at http://www.s.fpu.ac.jp/oka/appndrsra.pdf.

6. EXPECTED LOSS OF BIODIVERSITY FROM LOSING NAKAIKEMI WETLAND

Let us define the unit of biodiversity as the distance on the tree of the vascular plants from any terminal nodes to the root node, and let us express the contribution of a species <i>i</i> to the biodiversity in terms of this unit as <i>B<sub>i</sub></i>. The values of <i>B<sub>i</sub></i> are equal to the expected number of nodes below the upper taxon, for example, 3 for <i>Isoetes japonica</i> in Table II.
values for \( E_k[1/(m + k)] \) or \((m + 1/E_k[1/k])^{-1}\) in Table II. Because we assume an ultrametric tree, we may express the contribution of a species to biodiversity in terms of years on the assumption that, for example, the first diversion of vascular plants occurred 400 million years ago.\(^{24,25}\) Let \( Y_i \) represent the contribution of species \( i \) in this term, and then \( Y_i = B_i \times 4 \times 10^8 \).

Provided \( \Delta P_i \) is the increase in the extinction probability of species \( i \), namely \( \Delta(1/T) \) for species \( i \), then \( \Sigma \Delta P_i B_i \) or \( \Sigma \Delta P_i Y_i \) represents the ELB.\(^6\) The values for \( \Delta P_i Y_i \) are presented in the last column of Table II. The resulting ELB is about 9.200 years. This means Nakaikemi has a heritage of 9,200 years, which will be lost if this wetland disappears.

7. BENEFITS FROM THE DEVELOPMENT OF NAKAIKEMI WETLAND AND RISK–BENEFIT ANALYSIS

7.1. Treatment of the Conservation Area

A factor that makes the risk–benefit analysis of the development of Nakaikemi complicated is the difficulty in evaluating the conservation area with respect to ecological risk. Several threatened and rare species have been transplanted into the conservation area of 3.3 ha, and management including cultivation is being carried out in order to prevent succession.

One extreme view is to regard the nature of the wetland as perfectly conserved by this conservation area on the grounds that populations of the threatened species will be maintained there. However, this is disputed due to the following:

1. The success of the transplant is uncertain because the ecology of aquatic plants is not well known and a 3-year test is not sufficient.
2. The success of introducing insects and other animals is much more uncertain.
3. The potential capacity of maintaining biodiversity must be smaller in a human-controlled conservation area of 3.3 ha than in an ecosystem on an area of 25 ha unintendedly brought about as a by-product of human activities.

Another extreme view, considering these points, is to regard the ecosystem of Nakaikemi as being totally lost in the development in spite of the conservation area. Depending on these two extremes, the ELB of the development of Nakaikemi would become zero or 9,200 years. Here, we will show that a risk–benefit analysis can be done for both points of view.

7.2. Risk–Benefit Analysis: When the Conservation Area Is Regarded as Maintaining Diversity

When the conservation area is regarded as maintaining diversity, the ELB of the development becomes zero. This conservation entails cost, and this cost can be regarded as the benefit loss from the conservation. The initial investment cost for the conservation area is 1 billion yen, and its running cost is 60 million yen per year. Assuming a 25-year depreciation period and 3% discount rate, the total annual cost becomes 120 million yen. Consequently, the benefit–risk ratio (B/R ratio) for this conservation will be 13,000 yen per year-ELB (1 US dollar = 110 yen in 1999).

7.3. Risk–Benefit Analysis: When the Development Is Regarded as Causing Loss of All the Biodiversity of the Wetland

When the conservation area is not regarded as maintaining diversity, then this development is regarded as bringing about some benefit at the expense of 9,200 years of ELB. The benefit from the development will be estimated as the loss in consumers’ sur-
Expected Loss of Biodiversity

plus and the producer’s profit if the LNG plant is not constructed, or as the increase in the cost to construct the LNG plant at another site. Theoretically, the minimum of these two estimates should be regarded as the benefit from the development of Nakaikemi, and because the loss in consumers’ surplus and the producer’s profit will become considerably larger than the cost increase for constructing at another site, the benefit was estimated according to the latter concept.

To estimate the increase in construction cost as a result of rejecting Nakaikemi as the plant site, three alternative plans were assumed:

1. to construct the LNG plant adjacent to a new port for LNG tankers, which is as far from the main consumption area as Tsuruga;
2. to construct the LNG plant at the industrial park adjacent to Fukui Port; and
3. to utilize the reclaimed land, which was used for a coal gas plant, located at the outlet of the Yamato River (Osaka).

All these plans are thought to entail larger costs than the original plan. The first one has a disadvantage because it would require a new port for LNG tankers, whereas Nakaikemi is near the existing Tsuruga Port, for which expansion is now being undertaken. In the second plan, the LNG plant would be 75 km further from the consumption area than Tsuruga, which would raise the construction cost of the pipelines. In this plan, additional investment for improving the port would also be necessary. The third plan would require dredging for the port and the sea road, and is confronted with the problem of constructing pipelines in that they have to be built under heavily congested urban areas.

The increase in the construction cost was estimated to be 27 to 47 billion yen for the first plan, 91 to 100 billion yen for the second plan, and 36 to 44 billion yen for the third plan. On the assumption of a discount rate of 3% and a depreciation period of 50 years, the annual value for the cost increase ranges from 1.0 to 3.9 billion yen. This result means that the development of Nakaikemi would bring about the benefit of 1.0–3.9 billion yen at the expense of 9,200 years of ELB. The B/R ratio is 110,000 to 420,000 yen per year-ELB.

8. DISCUSSION

8.1. For What Purpose Is Our Method Useful?

Our results on ELB and the B/R ratio become meaningful when they are compared with the corresponding values for other places, other development plans, or other conservation policies. First, to compare ELB among several places would be useful for putting nature conservation policy on rational grounds. Our study on Nakaikemi is the first attempt to estimate ELB for a particular place, but it would not be difficult to apply the method developed here to other places. In fact, Matsuda et al. (26) has estimated the increments in the extinction risks of vascular plants due to the World Exposition 2005 (Expo 2005) planned in Kaisho Forest (540ha), Aichi Prefecture, Japan. The estimated values for the increments in the reciprocal of the time for extinction, $\Delta(1/T)$, are shown in Table III. ELB is calculated by summing up the values for $\Delta(1/T)$ with the diversity weight for each species. The resulting ELB is 230. Consequently, we can say that the ELB of Nakaikemi with an area of only 25 ha would be larger than the ELB of the Expo 2005 site with an area of 540 ha.

Second, a comparison of the B/R ratio would lead to a more cost-effective choice of conservation or development policy. Such a cost-effectiveness index should be taken into consideration when deciding on a development plan among several alternative plans for a project, whereas in the case of OGC’s LNG plant, an environmental impact assessment was carried out for just one development plan that had no alternatives. Our index ELB and the cost-effectiveness index based on it will provide a useful tool for improving the decision-making process.

### Table III. Expected Loss of Biodiversity (ELB) of the World Exposition 2005 Planned in Kaisho Forest

<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>$\Delta(1/T)$</th>
<th>Contribution to biodiversity (year)</th>
<th>ELB (year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Salvia isensis</td>
<td>$5 \times 10^{-5}$</td>
<td>3,400,000</td>
<td>170</td>
</tr>
<tr>
<td>2</td>
<td>Siphonostegia laeta</td>
<td>$2 \times 10^{-6}$</td>
<td>3,900,000</td>
<td>7.7</td>
</tr>
<tr>
<td>3</td>
<td>Eularia speciosa</td>
<td>$2 \times 10^{-6}$</td>
<td>3,100,000</td>
<td>6.2</td>
</tr>
<tr>
<td>4</td>
<td>Najas japonica</td>
<td>$3 \times 10^{-6}$</td>
<td>12,000,000</td>
<td>35</td>
</tr>
<tr>
<td>5</td>
<td>Magnolia tomentosa</td>
<td>$3 \times 10^{-7}$</td>
<td>12,000,000</td>
<td>3.5</td>
</tr>
<tr>
<td>6</td>
<td>Agrostis valvata</td>
<td>$2 \times 10^{-7}$</td>
<td>3,100,000</td>
<td>0.62</td>
</tr>
<tr>
<td>7</td>
<td>Najas indica</td>
<td>$7 \times 10^{-7}$</td>
<td>12,000,000</td>
<td>8.1</td>
</tr>
<tr>
<td>8</td>
<td>Bleilla striata</td>
<td>$1 \times 10^{-7}$</td>
<td>2,200,000</td>
<td>0.22</td>
</tr>
<tr>
<td>9</td>
<td>Alnus trabeculosa</td>
<td>$9 \times 10^{-8}$</td>
<td>9,500,000</td>
<td>0.86</td>
</tr>
<tr>
<td>10</td>
<td>Gastrodia pubilabiata</td>
<td>$9 \times 10^{-8}$</td>
<td>2,200,000</td>
<td>0.20</td>
</tr>
<tr>
<td>11</td>
<td>Cephalanthra falcata</td>
<td>$3 \times 10^{-8}$</td>
<td>2,200,000</td>
<td>0.07</td>
</tr>
<tr>
<td>12</td>
<td>Ajuga makinii</td>
<td>$1 \times 10^{-8}$</td>
<td>3,400,000</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Note: $\Delta(1/T)$ was calculated by Matsuda et al. (26)
8.2. National or Local Extinction and Worldwide Biodiversity

One problem with our approach is the fact that extinction of a species refers to nationwide extinction in Japan. This is due to the fact that the Red List, on which our calculation is based, deals with national extinction. The extinction simulation is based on the comprehensive and detailed data for 2,100 threatened plant species on the number of sites where each species exists, the population size at each site, and the nationwide distribution of the reduction rates of the population in the past 10 years. Such data are not available for the global level.

Dealing with only national extinction would also be justified if one consider that extinction in a country matters because the populations of a species in this country does contribute to global biodiversity to some but lesser extent than the species as a whole does. In principle, one can deal with contribution of any local population of a species to the global diversity in the same manner. However, in our present state of knowledge, it is difficult to quantify the contribution of national or local populations to the diversity, and it is difficult to make any assumption about the state of a species in other countries. Taking these things into account, our treatment in this study would be the best one for the moment.

8.3. What Aspects of Ecological Risk Are Excluded from ELB?

Our approach might give the impression of having an extremely simplified concept of biodiversity and the values of the ecosystem. Certainly, we captured biodiversity at the species level and measured it according to the phylogenetic distance to other species. In doing so, we excluded any functional values of species in the ecosystem and for human beings. It can be argued that the ecological function of a species or its usefulness for human beings is more important than phylogenetic uniqueness. However, our knowledge of species’ ecological function or usefulness for humans is too poor to be used for weighting species. Rather, when the function of a species in the ecosystem is important, it should be taken into account at the stage of assessing the increments in the extinction probabilities. In fact, our assessment of the increments in the extinction probabilities is based on the simulation for the Red List, and the simulation is based on the data about the trend of the populations in the last 10 years, which are thought to reflect the functional relations among species in the ecosystem.

We also excluded the concepts of ecosystem diversity and landscape diversity and concentrated on species diversity when constructing the measure of biodiversity. It can be argued that our measure would justify such a policy as to preserve a particular species under human control in isolation from the environment, or just to preserve genetic information of a particular species. We do not regard our measure of biodiversity in such a way. It is certainly a measure of genetic diversity in the sense that it reflects phylogenetic distance between species, but we think it makes sense only when genetic information is carried by living things and the living things exist in the natural ecosystem. Only in this way will the genetic and species diversity represent the diversity of the environment as a whole. In this sense, the preservation of species diversity is not the goal, but an indicator of the diversity of the environment as a whole, which is the ultimate object of preservation.

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REFERENCES


