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# Is there a positive relationship between naturalness and genetic diversity in forest tree communities?

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## Abstract

The concepts of genetic diversity and naturalness are well known as measures of conservation values and as descriptors of state or condition. A lack of research evaluating the relationship between genetic diversity and naturalness in biological communities, along with the possible implications in terms of evolutionary aspects and conservation management, make this subject particularly important as regards forest tree communities. We therefore examined the following hypothesis: the genetic diversity of a central-European tree stand averaged over species increases with the naturalness of the stand, as defined by the Potential Natural Vegetation (PNV). The results obtained show that the hypothesis is unsustainable because differences between the averaged genetic diversities of the unnatural and semi-natural stand classes (69 cases) were mostly non-significant. Moreover in three cases, the average genetic diversity of unnatural stand classes was significantly higher than the average genetic diversity of the semi-natural stand classes. A significantly lower average genetic diversity of unnatural stand class was not detected in the statistical analysis. Thus, the naturalness of a tree species community, as inferred from PNV, does not serve as a straightforward indicator of ecological stability when the genetic diversity and the adaptability of tree species are unknown.

**Key words**: Potential Natural Vegetation, isozyme, permutation test, transspecific genetic diversity, intermediate disturbance hypothesis.

## Resumen

### ¿Existe relación positiva entre la naturalidad y la diversidad genética en comunidades de árboles forestales?

Los conceptos diversidad genética y grado de naturalidad son bien conocidos como medidas de conservación y como descriptores del estado o condición actual. La carencia de estudios que evalúen la relación entre la diversidad genética y el grado de naturalidad en comunidades biológicas, así como sus posibles implicaciones en aspectos evolutivos y en el manejo con fines de conservación, hace este tópico particularmente importante especialmente en comunidades de árboles forestales. Por lo tanto, en este estudio se examinó la hipótesis siguiente: la diversidad genética de un rodal forestal en Europa central aumenta con el grado de naturalidad, de acuerdo con la definición del Potencial de Vegetación Natural (PNV). Los resultados muestran que la hipótesis es insostenible, porque las diferencias entre los promedios de la diversidad genética de los rodales con mayor grado de intervención del hombre (artificiales) y los seminaturales (69 casos) fueron en su mayoría no significativas. Además, en tres casos la diversidad genética promedio de las clases de rodales artificiales fue significativamente más alta que la diversidad genética promedio de los rodales seminaturales. El análisis estadístico indicó que ninguna de las clases de rodales artificiales evaluadas presentó una diversidad genética estadísticamente menor que las clases de rodales seminaturales. Por lo tanto, el grado de naturalidad de una comunidad forestal, inferido a partir de su PNV, no puede utilizarse como un indicador sencillo de la estabilidad ecológica cuando se desconoce la diversidad genética y la adaptabilidad de las especies arbóreas.

**Palabras clave**: Potencial de Vegetación Natural, isoenzima, prueba de permutaciones, diversidad genética transespecifica, hipótesis de disturbio intermedio.

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# Introduction

The concepts of biodiversity and naturalness are well known as measures of conservation values and as descriptors of state, or condition (Gregorius, 1987; Machado, 2004). Noss (1990) proposed one of the most comprehensive definitions of biodiversity by describing the term 'biological diversity' as the variety and variability among living organisms and the ecological complexes in which they occur and that can be classified in four hierarchical categories of biological organization: regional landscape, community-ecosystem, population-species, and genetic. In this regard, genetic diversity is the basis of all diversity levels (Gregorius et al., 2003) and is associated with the adaptability of a biological system (Gregorius, 2001). The average genetic diversity for plant communities can be measured by calculating the so-called 'transspecific genetic diversity' per species in a community (see Gregorius et al., 2003; Wehenkel et al., 2006; Wehenkel, 2007).

In the context of conservation biology, the concept of naturalness is used to define anything that has not been made or influenced by humans (Hunter, 1996; Angermeier, 2000). Some measurements and classifications of naturalness have been proposed (Machado, 2004). All measurements are confounded by the dilemma that maximal naturalness is unknown. The mere presence of a human observer in a study site, along with cumulative and ever-increasing societal effects, such as human-derived global climate change, pollution, etc. have undoubtedly reduced the level of naturalness at all sites across the planet. The designation and characterization of all biotic and abiotic elements also present practical problems in measuring and classifying naturalness. Most methods of evaluating naturalness described in the relevant literature involve classification of human intervention (artificiality, ruderality, etc.), and few are directly based on naturalness, e.g. according to the potential natural vegetation (for reviews see e.g. Bartha, 2004; Machado, 2004). However, the classification of human intervention is problematic because human-derived changes in conditions may result in a new and higher degree of naturalness (e.g. resettlement of potential native species; Hofmann, 1995). Furthermore, classification based directly on naturalness involves some conceptual errors. For example, the maximal naturalness corresponding to potential natural vegetation in an undisturbed situation cannot be teleologically linked to a climax situation because natural disturbances may revert ecosystems to early or intermediate successional states, which are as natural as the mature states (Machado, 2004). Until now, methods of measuring naturalness on the genetic level have failed, because actual and ideal values are unpredictable (Kleinschmit et al., 2004).

A lack of research evaluating the relationship between genetic diversity and naturalness in biological communities, along with the possible implications in terms of evolutionary and conservation management aspects make this subject particularly important as regards forest tree communities. We therefore examined the following hypothesis: The genetic diversity of a tree stand averaged over species increases with the naturalness of the stand, as defined by the Potential Natural Vegetation (PNV; Ellenberg, 1986), because naturalness acts to stabilize through higher adaptadness and adaptability of the population. Reason dictates that both mechanisms require sufficient genetic variation.

# Materials and methods

## Study sites and populations studied

The forest tree stands studied are located in the Thuringian forest area in Germany, in Central Europe. The stands are composed of different tree and shrub species that have been exposed to varied human influence. Nine stands were subdivided into six plots, each 40 x 40 m. For statistical purposes, only species represented by 15 or more individuals were included in the surveys. The tree species investigated, the total number of individuals per species, and the frequency of occurrence of individuals of each species in the nine stands are listed in Table 1. Apart from the three climax species (belonging to the genera *Abies, Picea* and *Fagus*), two pioneer species (of the genera *Betula* and *Pinus*), and five so-called admixed tree species (of the genera *Acer, Carpinus, Rhamnus, Sorbus,* and *Tilia*) were included in the study.

# Methods

## Genetic traits

Starch gel electrophoresis was used to assay five enzyme systems: aspartate aminotransferase (AAT, E.C. 2.6.1.1), hexokinase (HEK, E.C. 2.7.1.1), phosphoglucose isomerase (PGI, E.C. 5.1.3.9), malate dehydrogenase (MDH, E.C. 1.1.1.37), and isocitrate dehydroge-

**Table 1.** Tree species investigated, the total number of individuals per species, and the frequency of occurrence of each species within the stands.

| Species | Total number | Occurrence in stands |
|---|---|---|
| *Fagus sylvatica L.* | 2273 | 5 |
| *Picea abies L.* | 2108 | 6 |
| *Acer pseudoplatanus L.* | 562 | 3 |
| *Tilia cordata M.* | 227 | 2 |
| *Betula pendula Roth* | 176 | 1 |
| *Abies alba L.* | 55 | 2 |
| *Pinus sylvestris L.* | 52 | 1 |
| *Carpinus betulus L.* | 29 | 1 |
| *Rhamnus frangula L.* | 22 | 1 |
| *Sorbus aucuparia L.* | 19 | 2 |

nase (IDH, E.C. 1.1.1.42). In most cases, dormant buds were homogenized with a dithiothreitol-based buffer and the homogenates were processed directly on the starch gels. For further details of the electrophorestic procedures and staining recipes, see Konnert and Maurer (1995).

Thereafter, DNA data were obtained by amplified fragment length polymorphism (AFLP) technology. AFLP fingerprints were generated by use of the modified protocol described by Vos *et al.* (1995). The genomic DNA was extracted from dormant buds by QIAGEN DNeasy96 plant kit. AFLP markers were assayed as previously described by Markussen et al. (2005), with the following modifications: 250 ng DNA was digested in 50 µl with the enzyme combination PstI/MseI for 2 h, then ligated to the respective adapters. Ten microlitres of the ligation reaction were amplified for 20 cycles at 94ºC for 30s, 60ºC for 30s and 72ºC for 60s using AFLP primers with an extension of one nucleotide. The PCR product was diluted 5-fold and 5 µl of the dilution was used for the second amplification with AFLP primers containing three selective nucleotides (recognition sequence). In this study the AFLP primer PstI has been extended by the recognition sequence CCA, while the respective sequence of MseI reads CAG. The second PCR reaction was performed with the following thermal profile: Starting with an initial annealing temperature of 65ºC for 30s, two subsequent cycles at 64ºC, 62ºC and 58ºC, respectively were completed by 23 cycles at 56ºC. Each cycle lasted for 30s. Finally, 8.5 µl reaction products were resolved on high-resolution polyacrylamide gels on the automatic sequencer AFLexpress II and fragments were detected and analysed by using the Fragment Analyser software (Version 1.03, Amersham-Pharmacia).

Because inheritance studies were not performed (and are not required) for all tree species, the isozyme and AFLP patterns of all individuals were regarded as genetic traits, so that each individual could be characterized by its multilocus genotype, irrespective of the actual number of underlying gene loci and alleles per locus. However, the measurement of genetic variation for enzyme systems as well as the AFLP trait is based on individual phenotypic patterns. For purposes of comparison, the electrophoretic patterns of each genetic marker (trait) were generated by the same method, irrespective of the trait 'species' and therefore corresponding to the definition of transspecific genetic traits (see Gregorius et al., 2003). It should be considered that isozymes are functional traits of which the patterns reveal differences in charge and size. Hence, the same patterns found in different species evaluated by the same approach are herein interpreted as being functional. In contrast with the isozyme traits, it is believed to be mostly selectively neutral (but see Jump et al., 2006).

Not all individuals could be fully scored for each genetic trait and some produced non-informative scores. In the analysis of each genetic trait, these individuals were removed from the sample. This is justified under the realistic assumption that non-informative scores are unlikely to be produced by particular genotypes controlling the trait. For the MDH trait, two species (*Acer pseudoplatanus* L. and *Rhamnus frangula* L.), for the IDH trait, one relatively rare species (*Carpinus betulus* L.), and for the AFLP trait, two relatively rare species (*Tilia cordata* M. and *Sorbus aucuparia* L.) completely failed to produce informative scores in the study and were therefore excluded from the analysis.

## Measures of diversity and naturalness

All intraspecific genetic diversities based on the tree species investigated (Table 1) were calculated by so-called diversity profile $v_a$, where $a$ is a real number ranging from zero to infinity (Hill, 1973; Gregorius, 1978). The general concept underlying $v_a$ is roughly that the more frequent types determine the diversity of a collection to a greater degree than the less frequent types, and that the extent to which this is true increases with increasing parameter $a$. Among the most desirable characteristics of a measure of diversity is that, irrespective of the value of $a$, $v_a$ satisfies the requirement that (i) for a given number of types it assumes its largest value exactly when all these types are equally frequent, and this value equals the number of types, (ii) it increases as two types approach equal frequencies, and (iii) it increases when one type is subdivided into several subtypes.

Considered as a function of $a$, $v_a$ describes a diversity profile for each frequency distribution. The most illustrative values of the subscript $a$ in such a diversity profile are (i) $a = 0$, where the diversity is equivalent to the total number of variants; (ii) $a = 2$ as the effective number used in most genetic studies; and (iii) $a = \infty$, where only the most frequent variant determines the diversity. In the present study, the diversity profiles are represented by these three diversities for each collection. In this manner each population was characterized by the *total* number, the *effective* number, as inherent in Simpson diversity ($v_2=1/\sum_i p_i^2$), and the amount of *prevalent* variants (Gregorius, 1978).

Initially, the intraspecific genetic diversity of single species ($v_{a,g}$) per stand was measured. The genetic diversity of the community was calculated by the transspecific genetic diversity ($v_{a,tg}$) and the transspecific genetic diversity per species ($v_{a,tg}/v_{a,species}$) (Gregorius et al., 2003). The transspecific genetic diversity is defined as a measure of variation across the species boundary, i.e. all genetic variants, irrespective of their species affiliation, are considered equally. The effect of the species diversity ($v_{a,species}$) on the transspecific genetic diversity ($v_{a,tg}$) is eliminated when $v_{a,tg}$ is divided by the species diversity (per species; $v_{a,tg}/v_{a,Species}$). This implies that the frequencies of all variants of a genetic trait are regarded as units entering the same diversity measure (see $v_a$ above). Thus,

$$v_{a,tg}/v_{a,Species} = \frac{v_{a,tg}(p)}{v_{a,Art}(p)} = \left[\frac{\left(\sum_{s,i}(p_s p_{i,s})^a\right)}{\left(\sum_s p_s^a\right)}\right]^{\frac{1}{1-a}} \qquad [1]$$

where $p_{i,s}$: frequency of genetic variant $i$ within the species $s$, $p_s$: frequency of the species $s$ in the tree stand, $a \geq 0$, $a \neq 1$).

Because of the reduction of effects of sample size and, therefore, a better comparison of diversities between tree stands with different sample sizes (Table 1), we standardized the dataset by means of *averaged individual-based rarefaction curves* developed from 10,000 potential *individual-based rarefaction curves* (Gotelli and Colwell, 2001). Derived from this curves, the diversities per stand were calculated on the base of 100 individuals for the isozyme traits as well as 60 individuals for the AFLP traits.

The degrees of stand naturalness were classified according to the Potential Natural Vegetation (PNV). Here, the PNV is an imaginary state of vegetation, which (i) is in accord with the actual natural or anthropogenically irreversibly modified conditions with respect to location and (ii) is not a more human-induced state (Ellenberg, 1986; Jahn, 1995). The Potential Natural Vegetation was derived from cognitions (sensu Ellenberg, 1986) of local conditions and vegetation. Specifically, the PNV was defined by dominant, so-called admixed and subordinate concomitant tree species. Five degrees of naturalness were distinguished in the present study: (I) highly artificial (man-made), (II) moderately artificial, (III) moderately semi-natural, (IV) semi-natural, and (V) highly semi-natural. With this definition the ideal naturalness of forests is equated with the PNV of the climax state, and the last successional state is considered the most natural.

Because of the small sample size (nine stands), we initially included the highly artificial, moderately artificial and moderately semi-natural stands in the unnatural stand class (five stands) and the semi-natural and highly semi-natural stands in the semi-natural stand class (four stands). For purposes of comparison, we then considered the highly artificial and moderately artificial stands as unnatural stands (two stands), and the moderately semi-natural, semi-natural and highly semi-natural stands as semi-natural stands (seven stands).

In order to check whether the observed differences of the averaged genetic diversities (*Diff*) ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) between the unnatural and semi-natural created stand classes are produced solely by random events rather than directed forces, a permutation test based on randomly chosen reassignments was performed (Manly, 1997). This permutation test constitutes a non-parametric approach, which among other uses allows comparison of two groups in terms of the mean values of some variable, but unlike with the *t* test the assumptions of normality and equality of variances do not need to be satisfied by the data.

Essentially, the method involves generating a large enough number of reassignments (permutations) of individuals over unnatural and semi-natural stand classes and computing the ($v_{a,g}$), ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) genetic diversities for each reassignment. This yields a distribution of imitated ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) values.

This distribution is compared with the observed average value of the unnatural or semi-natural stand class. The percentages of imitated differences of ($v_{a,g}$), ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) genetic diversities (*Diff*) greater than or equal to the respective observed differences of genetic diversities (*P(Z≥Diff)*-values) need to be calculated. Consequently, if the *P(Z ≥ Diff)* is non-significant (for example $P > 0.05$), we can expect random-differences otherwise directed forces between the two stand classes.

## Results

Figure 1 shows a non-relationship between degree of naturalness classified according to the Potential Natural Vegetation (PNV) and the averaged transspecific genetic diversities per species ($v_{a,tg}/v_{a,species}$) for a = 0, a =2 and a = ∞ for the six genetic traits. The largest sum of the averaged transspecific genetic diversities per species was found for the degree of naturalness classified as moderately semi-natural.

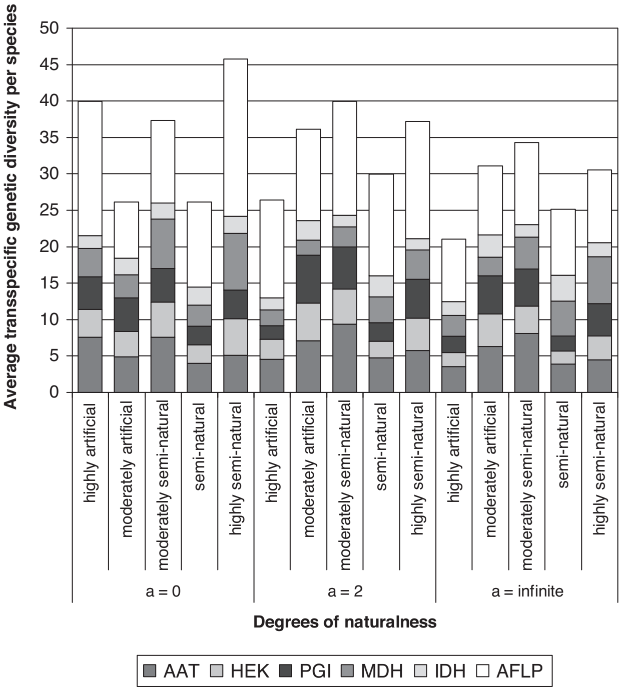

**Figure 1.** Relationship between the degree of naturalness classified according to their Potential Natural Vegetation (PNV) and the average of transspecific genetic diversities per species ($v_{a,tg}/v_{a,species}$) for a = 0, a =2 and a = ∞ in the AAT, HEK, PGI, MDH, and IDH enzyme systems as well as for the AFLP trait.

Tables 2 – 5 illustrate the probability of error *P(Z ≥ Diff)* for differences in the averaged genetic diversities ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) between the unnatural and semi-natural stands classes for the six genetic traits, for $a = 0$, $a = 2$, and $a = \infty$, respectively, each calculated from 10,000 permutations. The results clearly show that when the moderately semi-natural stands were included in the unnatural stand class then there were some statistically significant differences in the average transspecific genetic diversities per species ($v_{a,tg}/v_{a,species}$) between the unnatural and semi-natural stand classes, at the HEK and PGI enzyme systems (Tables 2 and 4). However, there were no statistically significant differences between the average genetic diversities ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) for the AAT, MDH, IDH, and AFLP traits. A statistically significant difference (i.e. a positive relationship) between the average genetic diversities was not observed.

When the moderately semi-natural stands were situated in the unnatural stand class, in three cases the values of the genetic diversities ($v_{a,tg}$) and ($v_{a,tg}/v_{a,species}$) were significantly higher than in the semi-natural stand class.

We did not observe significant differences between the intraspecific genetic diversities ($v_{a,g}$).

## Discussion and conclusions

The hypothesis, i.e. that the genetic diversity of a tree stand averaged over species increases with the naturalness of the stand, as defined by the PNV, is unsustainable because differences between the averaged genetic diversities of the unnatural and semi-natural stand classes (69 cases) were mostly non-significant. Moreover in three cases (in the HEK and PGI enzyme system), the averaged genetic diversity of unnatural stand classes was significantly higher than for the semi-natural stand classes (i.e. a negative relationship). A significantly smaller average genetic diversity of unnatural stand class (i.e. a positive relationship) was not detected in our study. For probabilities of error *P(Z≥Diff)* ≤ 0.100, in 12 cases (for the AAT, HEK, and PGI traits), the genetic diversity of unnatural stand classes was higher than for the semi-natural stand classes, and in only two cases it was smaller (for the MDH trait).

These results are consistent with the observed different isozyme diversity values of the participating tree species (inferred from several isozyme-gene systems). The average intraspecific genotype diversities of

**Table 2.** Probabilities of error *P(Z≥Diff)* for differences between the averaged transspecific genetic diversities ($v_{a,tg}$) in the first unnatural stand class (i.e. the highly artificial, moderately artificial and moderately semi-natural stands) and the first semi-natural stand class (i.e. semi-natural and highly semi-natural stands) in the AAT, HEK, PGI, MDH, and IDH enzyme systems as well as for the AFLP trait, for $a = 0$, $a = 2$, and $a = \infty$, each calculated from 10,000 permutations.

| a | $p_{AAT}$ | $p_{HEK}$ | $p_{PGI}$ | $p_{MDH}$ | $p_{IDH}$ | $p_{AFLP}$ |
|---|---|---|---|---|---|---|
| **0** | 0.098 (-) | 0.100 (-) | 0.098 (-) | 0.463 (-) | 0.491 (+) | 0.202 (-) |
| **2** | 0.101 (-) | 0.078 (-) | 0.094 (-) | 0.136 (+) | 0.304 (+) | 0.110 (-) |
| ∞ | 0.101 (-) | 0.045* (-) | 0.100 (-) | 0.219 (+) | 0.323 (+) | 0.201 (-) |

Note: Asterisk (*) indicates a significant difference in the averaged genetic diversities between the unnatural class and semi-natural stands, at a probability level of 5%. The negative value (-) shows that the average transspecific genetic diversity ($v_{a,tg}$) for the unnatural stand class was higher than for the semi-natural stands. Plus (+) symbolizes that the average transspecific genetic diversity ($v_{a,tg}$) for the unnatural stand class was smaller than for the semi-natural stand class.

**Table 3.** Probabilities of error *P(Z≥Diff)* for differences between the averaged transspecific genetic diversities ($v_{a,tg}$) in the second unnatural stand class (i.e. the highly artificial and moderately artificial stands) and the second semi-natural stand class (i.e. moderately semi-natural, semi-natural and highly semi-natural stands) in the AAT, HEK, PGI, MDH, and IDH enzyme systems as well as for the AFLP trait, for $a = 0$, $a = 2$, and $a = \infty$, each calculated from 10,000 permutations.

| a | $p_{AAT}$ | $p_{HEK}$ | $p_{PGI}$ | $p_{MDH}$ | $p_{IDH}$ | $p_{AFLP}$ |
|---|---|---|---|---|---|---|
| **0** | 0.496 (+) | 0.436 (+) | 0.445 (+) | 0.168 (+) | 0.412 (-) | 0.353 (+) |
| **2** | 0.496 (+) | 0.474 (+) | 0.419 (+) | 0.140 (+) | 0.307 (-) | 0.414 (+) |
| ∞ | 0.496 (+) | 0.360 (+) | 0.607 (+) | 0.082 (+) | 0.280 (-) | 0.498 (+) |

isozymes of the pioneer species, *Betula pendula* ROTH and *Pinus sylvestris* L., were higher than for the climax species *Fagus sylvatica* L. and *Abies alba* MILL. The average intraspecific (genotype) isozyme diversities of the polyploid and admixed tree species, *Acer pseudoplatanus* L. and *Tilia cordata* M. were also higher. However, the genotype diversity of the same isozymes in *Picea abies* L. is comparatively small (see e.g. Wehenkel et al., 2006). With respect to genetic type frequencies, the traits IDH and MDH were distinguished from the other traits by comparatively low $v_{a,tg}$ with many rare genetic variants in most of the tree species investigated in this study. This constitutes a particular type of minor polymorphism at least partly caused the non-significant differences of $v_{a,tg}$ and $v_{a,tg}/v_{a,species}$ (Bergmann et al., 2008). We interpret the non-significant differences of the genetic diversities of the AFLP trait as their lower selective capability (mostly selectively neutral loci) in contrast to isozymes (Jump et al., 2006; Bergmann et al., 2008). With respect to the MDH, IDH and AFLP traits, the exclusion of some tree species from the analysis (see methods) could only affect the results, where the diversities are equivalent to the total number of variants (i.e. for $v_{0,tg}$ and $v_{0,tg}/v_{0species}$) because the absent species and their missing genetic variants were not prevalent. With increasing *a* in the diversity profile ($v_a$), only the most frequent variants determine the diversity.

Tree species with higher values of isozyme genotype diversities (*Betula pendula* ROTH*, Pinus sylvestris* L*, Acer pseudoplatanus* L.*,* and *Tilia cordata* M.) occurred more frequently in highly artificial, moderately artificial, and moderately semi-natural stands, than those species occurring in semi-natural and highly semi-natural stands in which there is sometimes a trade-off between the degree of naturalness and the genotype diversity. The higher frequencies of this species in unnatural stands may be due to their high adaptability to a variety of unpredictable environmental conditions and disturbances (Stern and Roche, 1974; Gregorius, 1996; Ziehe et al., 1999) and they are therefore able to quickly colonize forests with a history of anthropogenenic disturbance. The absence of the highly competitive climax specialist tree species, *Fagus sylvatica* L. and *Abies alba* MILL., which require optimal edaphic and microclimatic conditions - or differently expressed, less external disturbances (such as human intervention) (West et al., 1981; Wehenkel et al., 2006) also encourage rapid colonization. In case of the pioneer tree species, *Betula pendula* ROTH and *Pinus sylvestris* L. it is generally

**Table 4.** Probabilities of error $P(Z \geq Diff)$ for differences between the average transspecific genetic diversities per species ($\nu_{a,tg}/\nu_{a,species}$) in the first unnatural stand class (i.e. the highly artificial, moderately artificial and moderately semi-natural stands) and the first semi-natural stand class (i.e. semi-natural and highly semi-natural stands) in the AAT, HEK, PGI, MDH, and IDH enzyme systems as well as for the AFLP trait, for $a = 0$, $a = 2$, and $a = \infty$, each calculated from 10,000 permutations.

| a | $p_{AAT}$ | $p_{HEK}$ | $p_{PGI}$ | $p_{MDH}$ | $p_{IDH}$ | $p_{AFLP}$ |
|---|---|---|---|---|---|---|
| **0** | 0.069 (-) | 0.106 (-) | 0.045* (-) | 0.216 (-) | 0.119 (+) | 0.304 (+) |
| **2** | 0.124 (-) | 0.045* (-) | 0.129 (-) | 0.072 (+) | 0.115 (+) | 0.483 (-) |
| ∞ | 0.100 (-) | 0.106 (-) | 0.091 (-) | 0.123 (+) | 0.072 (+) | 0.335 (-) |

Note: Asterisk (*) indicates a significant difference in the averaged genetic diversities between the unnatural class and semi-natural stands, at a probability level of 5%. The negative value (-) shows that the average transspecific genetic diversity per species ($\nu_{a,tg}/\nu_{a,species}$) for the unnatural stand class was higher than for the semi-natural stand class. Plus (+) symbolizes that the average transspecific genetic diversity per species ($\nu_{a,tg}/\nu_{a,species}$) for the unnatural stand class was smaller than for the semi-natural stand class.

**Table 5.** Probabilities of error $P(Z \geq Diff)$ for differences between the averaged transspecific genetic diversities per species of species ($\nu_{a,tg}/\nu_{a,species}$) in the second unnatural stand class (i.e. the highly artificial and moderately artificial stands) and the second semi-natural stand class (i.e. moderately semi-natural, semi-natural and highly semi-natural stands) in the AAT, HEK, PGI, MDH, IDH enzyme systems as well as for the AFLP trait, for $a = 0$, $a = 2$, and $a = \infty$, each calculated from 10,000 permutations.

| a | $p_{AAT}$ | $p_{HEK}$ | $p_{PGI}$ | $p_{MDH}$ | $p_{IDH}$ | $p_{AFLP}$ |
|---|---|---|---|---|---|---|
| **0** | 0.416 (+) | 0.444 (+) | 0.279 (-) | 0.275 (+) | 0.161 (+) | 0.549 (+) |
| **2** | 0.467 (+) | 0.445 (+) | 0.528 (+) | 0.084 (+) | 0.502 (-) | 0.218 (+) |
| ∞ | 0.496 (+) | 0.330 (+) | 0.391 (+) | 0.082 (+) | 0.498 (-) | 0.368 (+) |

accepted that their wide ranges of distribution are associated with higher genetic diversity within their populations (see e.g. Hamrick et al., 1992).

Connell and Slatyer (1977) presented the intermediate disturbance model (hypothesis) that maximal species diversity accompanies intermediate disturbance. Our observation of trade-offs between naturalness and genetic diversity in some cases may extend the model beyond the species level, taking into account the genetic level, because unnatural tree stands have resulted from an intermediate (human) disturbance. The predominantly positive relationship between species diversity and the average genetic diversity of tree communities also support this conclusion (Vellend and Geber, 2005; Wehenkel et al., 2006).

Because of a trade-off between naturalness, as defined by the Potential Natural Vegetation, and genetic diversity of tested tree stands in some combinations (see Table 2 and 4), the degree of naturalness increases at the expense of adaptability of the tree community (Ziehe et al., 1999). This means that the tested semi-natural community may exhibit lower stability because of its lower adaptive capacity (Gregorius, 2001).

On the basis of the results of the present study, we conclude that the naturalness of a tree species community, as inferred from PNV, cannot generally serve as a straightforward universal indicator of ecological stability when the genetic diversity and the adaptability of tree species are not known.

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