The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem

MELODIE A. McGEOCH*, BERNDT J. VAN RENSBURG and ANTOINETTE BOTES

Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

Summary

1. Bioindicators of habitat quality and environmental change must be identified quantitatively and tested independently to confirm their usefulness. We used the indicator value (*IndVal*) method, which combines measures of habitat fidelity and specificity, to assess the indicator responses of dung beetles (Coleoptera: Scarabaeidae) in Tembe Elephant Park, South Africa. The indicator responses were verified by sampling in different areas of the Park, 2 years after the responses were originally quantified.

2. We postulated that terrestrial insect indicators with different combinations of habitat specificity and fidelity might fulfil different indicator roles. Indicator species with strong habitat specificity (characteristic species) are unlikely to provide information on the direction of ecological change despite high vulnerability. Rather, detector species that span a range of ecological states are likely to be better in this role. We used *IndVal* for selecting such detector species that indicate the direction of ecological change.

3. Sets of species were found to be robust bioindicators, i.e. reliably characteristic across the habitat of which they were indicative. The suite of indicators was refined by discarding those with *IndVal*s that varied significantly across years, thus improving the confidence in the final suite of species selected. By clearly responding to a change in habitat between two ecological states, detector species provided information complementary to that provided by characteristic species.

4. The *IndVal* method enabled both the identification and testing of indicator (characteristic and detector) species. Because of its resilience to changes in abundance, *IndVal* is a particularly effective tool for ecological bioindication.

5. We conclude that both characteristic and detector species are useful bioindicators of habitat quality and conversion. We propose that bioindicators that are categorized and verified in this way will have valuable application in the monitoring of habitat integrity.

Key-words: bioindication, detector species, habitat specificity, habitat transformation, indicator species, Scarabaeidae.

Journal of Applied Ecology (2002) **39**, 661–672

Introduction

For bioindicators to be used with confidence, they must be tested on data independent from those used for initial identification. Most ecological and environmental bioindicators are identified by establishing a strong relationship with some characteristic of their environment (Kitching *et al*. 2000; Davis 2001; for definitions

see McGeoch 1998). Once such a relationship has been established, its robustness should be tested, for example by resampling the same environment under different temporal or spatial conditions (Weaver 1995; Majer & Nichols 1998). This may involve sampling during a period with different weather conditions, or sampling elsewhere in the geographical region within which the bioindicator is to be used.

One method used to quantify the 'bioindicator value' of a range of taxa is the indicator value (*IndVal*) method developed by Dufrêne & Legendre (1997). This method combines measurements of the degree of specificity of a species to an ecological state, for

*Present address and correspondence: Melodie A. McGeoch, Department of Conservation Ecology, University of Stellenbosch, Private Bag X01, Matieland, 7602 South Africa (fax +27 21 8083304; e-mail mcgeoch@sun.ac.za).

M. A. McGeoch,
B. J. van Rensburg
& A. Botes

Fidelity

Fig. 1. Species characterized by a combination of their degree of environmental specificity and fidelity (similar to the classification by Rabinowitz 1981), and classified on this basis as either indicators [characteristic (Dufrêne & Legendre 1997) or detector (Jenkins 1971) species], tramp (Diamond 1975), rural (Kent *et al*. 1997) or vulnerable (Gaston 1994) species.

example a habitat type, and its fidelity within that state (Dufrêne & Legendre 1997). Species with a high specificity and high fidelity within a habitat will have a high indicator value (Fig. 1). High fidelity (frequency of occurrence) of a species across sample sites is generally associated with large abundance of individuals (Brown 1984; Gaston, Blackburn & Lawton 1997). Both these characteristics facilitate sampling and monitoring, which is an important requirement for a useful bioindicator (Jenkins 1971; Kremen, Merenlander & Murphy 1994).

The *IndVal* method has numerous advantages over other measures used for ecological bioindication (McGeoch & Chown 1998). For example, the *IndVal* is calculated independently for each species, and there are no restrictions on the way in which sites (habitats) are categorized, i.e. these may be grouped subjectively or quantitatively (McGeoch & Chown 1998). None the less, the usefulness of this method is ultimately dependent on the degree to which species maintain high and significant indicator values (*IndVal*s) when tested in different locations and times. Although habitat specificity is a comparatively inflexible species-specific trait (Southwood 1977; Greenslade 1983), the abundance of species (and thus their fidelity) in an assemblage may vary over time in at least two ways. The sensitivity of the *IndVal* to such changes will ultimately determine its usefulness for bioindication.

First, the abundance of all species in an assemblage may change with season and weather conditions (Wolda 1988; Kingsolver 1989; Tauber *et al*. 1998). Because the *IndVal* reflects frequency of occurrence (abundance), abundance changes are likely to alter year-to-year indicator values. However, the *IndVal* method may accommodate such abundance changes because *IndVal* is calculated by comparing a species' frequency of occurrence between habitat types, i.e. relative differences in frequency of occurrence between habitat types, rather than absolute values, determine the contribution of the fidelity component to the *IndVal*. Interannual

differences, for example in weather patterns, are thus likely to have only minor effects on the *IndVal* of a species if it is similarly affected by environmental variability across all the habitats in which it is found. Secondly, disturbance-induced environmental changes are likely to affect the abundance of some species in an assemblage more than others (Erhardt & Thomas 1991; Luff & Woiwod 1995; Steenkamp & Chown 1996). It is those species that are sensitive to such changes that are usually of conservation interest, and most valuable for monitoring a particular environmental or ecological state (Noss 1990). None the less, the degree to which the habitat specificity, fidelity and *IndVal* of these species are predictable over time has to be established before they can be used as bioindicators with a measurable degree of confidence.

The *IndVal* method, as proposed by Dufrêne & Legendre (1997), identifies indicator species as those 'characteristic' of a particular habitat (i.e. with high specificity and fidelity to the habitat and thus a high percentage *IndVal*; Fig. 1). However, species with other combinations of specificity and fidelity may also be useful indicators, for example detector species (Fig. 1). When monitoring environmental change, species that span a range of ecological states (i.e. do not have high specificity) may be more useful indicators of direction of change than highly specific (characteristic) species restricted to a single state (Fig. 1). Because habitat specificity is likely to be relatively resistant to change over time in comparison with population abundance levels, species are thus likely to move between the fidelity categories of Fig. 1 more readily than between specificity categories (Greenslade 1983; Doube 1987; McGeoch & Chown 1998). The abundance (and thus the fidelity) of characteristic species may decline rapidly under changing environmental conditions to the point where they are regarded as vulnerable (Fig. 1). These species will become increasingly difficult to sample (Fig. 1), and may disappear rapidly with no further value for monitoring thereafter. Characteristic indicator species also provide no information on the direction of ecological change (although changes in their abundance may remain useful for monitoring within the habitat to which they are specific), because they are highly specific and thus restricted to a single ecological state (Fig. 1). In contrast, species with moderate specificity levels (detector species; Fig. 1) may be more useful for monitoring change. Because the detector species have different degrees of preference for different ecological states, relative changes in their abundance across states may be indicative of the direction in which change is occurring. Furthermore, these species are less likely to become vulnerable than indicator species, because a variety of habitats or ecological states, rather than only a single one, provide suitable resources for them. Bioindication in aquatic and soil systems makes use of species such as these that have a range of preferences for different environmental states (Williams *et al*. 1986; Weatherley & Ormerod 1990; van Straalen & Verhoef

1997) but this distinction has less commonly been made in above-ground terrestrial bioindication.

Therefore, if detector species can be identified in assemblages, they will provide information complimentary to that provided by characteristic indicator species. Detector species will facilitate longer-term assessment, as well as indicate the direction in which ecological change is taking place. The two objectives of ecological bioindication outlined above are best addressed separately, i.e. the identification of characteristic, indicator species for monitoring within a particular ecological state, and the identification of detector species for monitoring within and across states to detect the direction in which change is occurring. These objectives should be addressed in a two-stage process involving the initial identification followed by the testing of the potential bioindicator (McGeoch 1998).

In this study, we followed such a two-stage process by testing the dung beetles identified as characteristic and detector species in a previous investigation (van Rensburg *et al*. 1999). Based on a study conducted over a full year in 1995–96, indicator species were identified from dung beetle assemblages in two habitat types in Tembe Elephant Park in northern KwaZulu-Natal, South Africa (van Rensburg *et al*. 1999). Dung beetle species characteristic of mixed woodland and sand forest habitats, and those that were predicted to be indicative of a change in habitat state from sand forest to mixed woodland, were selected using the *IndVal* method (Dufrêne & Legendre 1997). Sand forest is a restricted and threatened habitat type that, under disturbance conditions in the area (clearing for firewood, settlement, livestock grazing and intense use by elephants), is being replaced by mixed woodland (van Wyk 1996; van Rensburg *et al*. 1999). Patches of sand forest are characteristically embedded within a matrix of mixed woodland vegetation, and closed sand forest contributes significantly to the floral and faunal endemism of the area, known as the Maputuland Centre (van Wyk 1996; van Rensburg *et al*. 2000a). Differences in vegetation structure between the two habitats are thought to contribute most to the differences in dung beetle assemblages between them (van Rensburg *et al*. 1999; van Rensburg *et al*. 2000a). Disturbance to these habitats usually results in a more open structure and conversion to a mixed woodland habitat type. To date, no reversion to the original habitat structure has been recorded for disturbed patches of sand forest (van Rensburg *et al*. 1999).

The objectives of the present study were therefore to: (i) test the consistency of the indicator values of characteristic species in dung beetle assemblages in Tembe Elephant Park, and thus estimate the reliability of the chosen indicator species; (ii) examine the effect of differences in species abundance between studies on the specificity and fidelity components of *IndVal* measures; and (iii) test the responses of dung beetle species predicted to perform as detectors to a change in habitat type from sand forest to mixed woodland.

Methods

STUDY AREA

Sampling took place in Tembe Elephant Park (27°01′S 32°24′E) and adjacent, unprotected tribal land (27°00′S 32°18′E), on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. There is disturbed sand forest adjacent to the park where patches are inhabited by people at low to moderate densities. Sand forest is characterized by a closed canopy (van Wyk 1996) with a poorly developed understorey (van Wyk 1996). The surrounding, more open, mixed woodland is characterized by common, woody savanna species and a well-developed grass understorey (for further description of these habitats see van Rensburg *et al*. 1999).

SAMPLING AND SPECIES IDENTIFICATION

Dung beetles were used initially because they are sensitive to habitat change, have been suggested as potential indicators, and the fauna in the area is well known (Doube 1983; Klein 1989; Favila & Halffter 1997; Spector & Forsyth 1998; van Rensburg *et al*. 1999; Davis 2001). In the initial study by van Rensburg *et al*. (1999) replicated sampling sites were selected within standardized vegetation communities in Tembe Elephant Park (undisturbed sand forest and mixed woodland). During this study (i.e. 1995–96; van Rensburg *et al*. 1999) two sand forest sites and two mixed woodland sites in the Park were sampled bimonthly (i.e. each site was sampled six times over 12 months). These data were thus seasonally representative of the dung beetle fauna in the Park, and an asymptote to species richness was reached over this period (van Rensburg *et al*. 2000b).

To generate an independent data set, resampling was conducted in and adjacent to Tembe Elephant Park in December 1998, 32 months after the initial study. The two sampling periods (1995–96 and 1998) were separated by two summer rainfall periods, during which dung beetle activity is at a maximum. The December 1998 sample was conducted during a period when dung beetle activity was high (shortly after rainfall in early to mid-summer; Doube 1987). During this period, two sand forest sites and two mixed woodland sites inside the Park (different to those used in the initial study) were sampled once, and at the same time two disturbed sand forest sites were sampled outside of the Park. Tembe Elephant Park represented the undisturbed sand forest habitat, whereas the human-occupied tribal land adjacent to Tembe represented the disturbed sand forest. Five grids of six pitfalls each (six pitfalls in a 2×2-m grid) were placed in each habitat site sampled (van Rensburg *et al*. 1999, 2000b). Pitfall traps were baited with 50 g elephant dung. During each sample month of the 1995–96 study, the pitfalls were set once for 48 h, with rebaiting and the first collection taking

place at 24 h, and the second collection at 48 h (van Rensburg *et al.* 1999). In 1998, pitfalls were baited once and set for 24 h. The sample effort in December 1998 was thus one-twelfth of that of the full 1995–96 study. Specimens were identified by comparing them to identified specimens in the collections of the National Collection of Insects (Pretoria, South Africa).

The rationale for testing the bioindicator system using a single 24-h sample rather than an additional full year of sampling was as follows. Once an asymptote to species richness is reached for an area, sampling a single additional year is unlikely to contribute significantly to determining the equilibrium abundance for proposed indicator species (Dempster & McLean 1998). Numerous years, often including years with extreme natality and mortality levels, are necessary to estimate equilibrium abundance for species (Dempster & McLean 1998). However, the demand for bioindicators is immediate, and more rapid approaches to their selection and testing are therefore required (although this does not negate the necessity for rigorous testing procedures and longer-term monitoring; McGeoch 1998). The 1995–96 data set was thus regarded as sufficiently representative to serve as a reference data set for indicator species selection. Thereafter, a single sample, taken when the abundance of adults in the field reached its annual maximum, was used to test this bioindicator system, as this is likely to be the way in which monitoring over the longer term will be conducted. The majority of species in dung beetle assemblages are generally active at such periods, and present in sufficient numbers (Doube 1983) to allow the testing of indicator species identified from a more seasonally representative data set.

INDICATOR VALUES AND SPECIES

The numbers of individuals of each species trapped during the course of each study period (1995–96 and 1998) were summed for each sampling grid. Mean abundance and species richness was compared between sampling periods and habitat types using analysis of variance and Tukey's multiple comparison tests. Characteristic dung beetle species (Fig. 1) were identified for each habitat type and each sampling period using the indicator value method (Dufrêne & Legendre 1997). This method combines measures of specificity and fidelity and provides an *indicator value* (*IndVal*) for each species, as a percentage, as follows (Dufrêne & Legendre 1997):

specificity measure: $A_{ij} = Nindividuals_{ij}/Nindividuals_i$

where $Nindividuals_{ij}$ is the mean number of species *i* across sites of group *j*, and $Nindividuals_i$ is the sum of the mean numbers of individuals of species *i* over all groups;

fidelity measure: $B_{ij} = Nsites_{ij}/Nsites_j$

where $Nsites_{ij}$ is the number of sites in cluster (habitat) *j* where species *i* is present, and $Nsites_j$ is the total number of sites in that cluster.

The percentage indicator value for species *i* in cluster (habitat) *j* is then:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

The following *IndVal* analyses were conducted: (i) sand forest vs. mixed woodland for the May 1995 to April 1996 data (van Rensburg *et al.* 1999); (ii) sand forest vs. mixed woodland for the December 1998 data. Dufrêne & Legendre's (1997) random reallocation procedure of sites among site groups was used to test the significance of the *IndVal* measures for each species. Each species has a percentage *IndVal* with an associated measure of significance, with high and significant percentages designating good indicator species. Those species with significant *IndVal*s of greater than 70% (subjective benchmark; van Rensburg *et al.* 1999) were regarded as characteristic indicator species for the habitat in question. The site hierarchy component of Dufrêne & Legendre's (1997) method to select site clusters was not used here because the habitats for which characteristic species were required (sand forest and mixed woodland) were known a priori.

The number and identity of species in the sets of characteristic species identified for each habitat type from each of the two sampling periods (1995–96 and 1998) were then compared. *t*-tests were used to establish which of these species had *IndVal*s of significantly greater than 70% across the two sampling periods (Bulmer 1979). The relationship between the *IndVal*s of species in mixed woodland and sand forest in the two different sampling periods was tested using simple linear regressions with arcsine transformation of both response and predictor variables (appropriate for percentages; Collett 1991). The relationship between the *IndVal*s of species in 1995–96 and the change in *IndVal* for each species between 1995–96 and 1998 (|*IndVal* 1995–96 – *IndVal* 1998|) was similarly determined (with arcsine transformation). *IndVal* means and variances were calculated for each species from their *IndVal*s for the two studies (*n* = 2), and the relationship between the mean and variance was examined using simple linear regression. Only species sampled in both sample periods were included in the above analyses.

The relationships between the fidelity and specificity components of the *IndVal* (both are proportions) and species abundance were examined across habitats and sampling periods using linear logistic models (McCullagh & Nelder 1989; Collett 1991).

DETECTOR SPECIES

Species that were predicted to act as detectors of a change in habitat from sand forest to mixed woodland were identified as those species with *IndVal*s of between

Table 1. Dung beetle species richness and abundance from each habitat and sampling period

Habitat and sample	Richness (mean ± SE) $F_{4,45} = 27\cdot54$, $P < 0\cdot001$	Abundance (mean ± SE) $F_{4,45} = 10\cdot04$, $P < 0\cdot01$	n	S	N
Mixed woodland 1995–96	35·10 ± 1·73a	1239·00 ± 148·88ac	10	64	12390
Mixed woodland 1998	39·60 ± 2·35a	1886·80 ± 257·70a	10	65	18863
Sand forest 1995–96	22·10 ± 1·14b	839·40 ± 102·75bc	10	49	8394
Sand forest 1998	22·40 ± 1·69b	675·90 ± 110·04bc	10	39	6759
Disturbed sand forest 1998	19·60 ± 1·39b	543·20 ± 187·73b	10	45	5432

n = number of sample grids; S = total richness; N = total abundance. Different letters associated with each mean in each column denote significant differences between means of $P < 0\cdot05$.

50% and < 70% for mixed woodland, and between 5% and < 50% for sand forest from the 1995–96 data. These species were therefore not characteristic species, as they did not have high *IndVal*s of ≥ 70% for any particular habitat. However, species meeting these criteria were regarded as sufficiently indicative of mixed woodland to demonstrate an early shift in sand forest habitat towards a mixed woodland state. Simultaneously, these species were judged as sufficiently uncharacteristic of sand forest to show potentially a marked increase in indicator value in this habitat type under disturbance conditions.

The rationale for selecting potential detector species in this way is that first, reliable characteristic species (i.e. those with high specificity and fidelity, and as used here with significant *IndVal*s of > 70%) are unlikely to move from their requisite to other habitat types, even under changing conditions within this habitat. Populations of these species therefore need only be monitored within the habitat to which they are specific. Secondly, generalist (low specificity) species are also unlikely to respond very rapidly to changing habitat conditions. On the other hand, those species with some degree of habitat preference (as used here, those with significant *IndVal* measures of between 50% and 70% for mixed woodland and less for sand forest) are likely to move to adjacent habitats more rapidly under changing habitat conditions than either of the previous two categories. These detector species would thus be most likely to invade sand forest in the early stages of its change to a mixed woodland-like state. Detector species were selected from the May 1995 to April 1996 data set. The *IndVal*s of the 11 species (four with significant *IndVal*s for mixed woodland) in the assemblage that met the detector criteria were predicted to demonstrate the transformation of sand forest into mixed woodland. These were tested by including the 1998 disturbed sand forest data in two three-way habitat comparisons, i.e. *IndVal*s calculated from (i) mixed woodland and sand forest 1995–96 and disturbed sand forest 1998, and (ii) mixed woodland and sand forest 1998 and disturbed sand forest 1998. We predicted specifically that these detector species would be better indicators of disturbed than undisturbed sand forest, and in the combined analyses (i and ii above) that their *IndVal*s for the disturbed sand forest would be larger

than for sand forest. Therefore species originally selected as detectors were taken to have responded as predicted if their *IndVal*s for disturbed sand forest were higher than they were for sand forest (undisturbed) in the latter two analyses.

Results

In the single sample period of December 1998, 35% more dung beetle individuals were sampled than in the six equivalent sampling periods between 1995 and 1996 in mixed woodland in Tembe Elephant Park (Table 1). In contrast, 20% fewer individuals were sampled in sand forest in 1998 (in comparison with the 1995–96 sampling period; Table 1). Species richness was also substantially higher in the 1995–96 sampling period in sand forest than in 1998. None the less, neither mean species richness nor abundance were significantly different within habitat types between years (Table 1). Total species richness in disturbed sand forest was higher than in undisturbed sand forest in 1998, although lower than in undisturbed sand forest during 1995–96. In contrast, total dung beetle abundance was lower in disturbed than in undisturbed sand forest (Table 1). There was no significant difference in either mean species richness or abundance between disturbed and undisturbed sand forest (Table 1).

Thirteen species were recorded in the 1998 sample (independent data set) that had not been previously recorded, of which four were unique to disturbed sand forest (Appendix A; van Rensburg *et al.* 1999). The latter species were all omnivore dung specialists, commonly associated with human faeces (Davis 1994). No species were found that occurred in sand forest only across sampling periods, whereas five species were found only in mixed woodland in both sampling periods. However, none of these occurred sufficiently frequently or abundantly to be identified as characteristic or detector species.

INDICATOR VALUES AND CHARACTERISTIC SPECIES

More mixed woodland than sand forest species had high *IndVal*s (in both 1995–96 and 1998; Fig. 2). Also, there were in general more species with *IndVal*s of
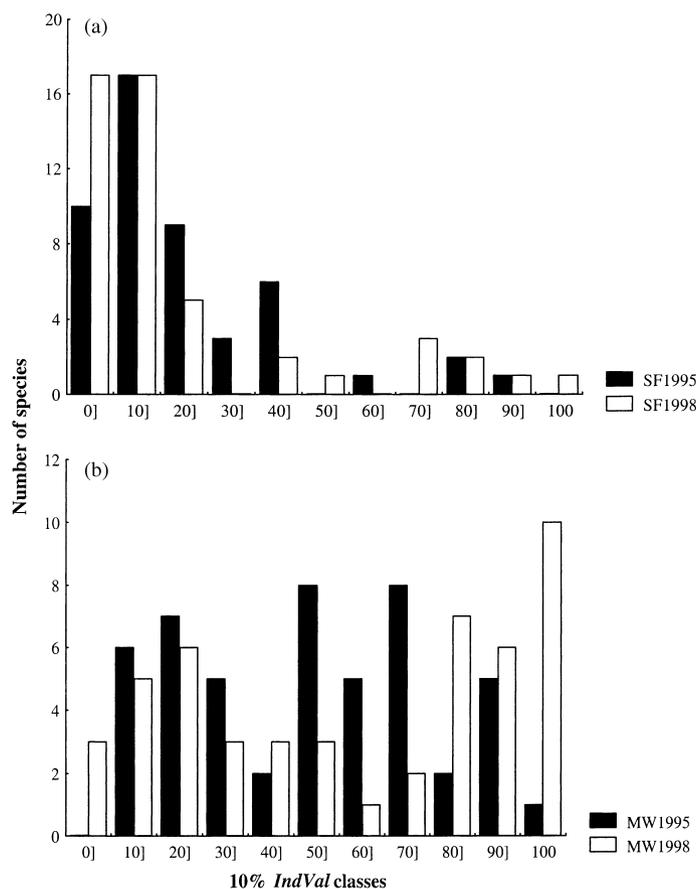
Fig. 2. The number of species in (a) sand forest (SF) and (b) mixed woodland (MW) in 1995–96 and 1998 with indicator values (% *IndVal*s) of zero, and thereafter in 10% category classes. Only species present in each habitat in both studies were included.

> 70% in 1998 than there were in 1995–96 (Fig. 2). The relationships between the *IndVal*s of species in the two sampling periods (1995–96 and in 1998) were significantly positive, although only between 15% and 46% of the variability in the data was explained by these relationships [mixed woodland: $F_{1,44} = 7·81$, $P < 0·008$, $R^2 = 0·15$, arcsine *IndVal* 1998 = 0·41 + 0·62(arcsine *IndVal* 1995–96); sand forest: $F_{1,29} = 24·89$, $P < 0·001$, $R^2 = 0·46$, arcsine *IndVal* (1998) = 0·04 + 0·98(arcsine *IndVal* 1995–96)]. The *IndVal* of a species in the first year was thus a poor to at best reasonable predictor of its *IndVal* in the following sample period.

However, the relationships between *IndVal*s in 1995–96 and the change in *IndVal*s of species between the two periods (1995–96 and 1998), although not significant for sand forest, were negative and triangular (*sensu* Thomson *et al*. 1996) (Fig. 3a,b). There was, on average, less change in the values of species with high *IndVal*s than those with low *IndVal*s in 1995–96. The values of species with *IndVal*s of above 70% in 1995–96 changed by between 0% and 35% (mixed woodland; Fig. 3a) and 13% and 18% (sand forest; Fig. 3b). The use of species with significant *IndVal*s of above 70% as bioindicators (as opposed to species with significant *IndVal*s < 70%) therefore has some empirical support.

The relationships between mean *IndVal*s and their variances were not significant for either habitat type.

However, in both habitats moderate *IndVal*s (between approximately 30% and 60%) had the highest and greatest range of variances, whereas very low and high *IndVal*s were substantially less variable (Fig. 4). This pattern may be expected when values are bounded in some way (in this case the *IndVal* lies between zero and 100).

Although more species emerged as indicator species (significant *IndVal*s of > 70%) in 1998 than in 1995–96, most of those species that were identified as indicators in 1995–96 reappeared as such in 1998 (Table 2). The exceptions were *Onthophagus lacustris* in sand forest and *Kheper lamarcki* in mixed woodland (Table 2), with mean *IndVal*s of less than 70% across both sampling periods. Therefore, one sand forest species and six mixed woodland species had *IndVal*s of significantly greater than 70% across both sampling periods (Table 2).

Species abundance was significantly positively related to the fidelity component of the *IndVal* (d.f. = 180, deviance = 48·38; abundance: d.f. = 1, $\chi^2 = 64·68$, $P < 0·001$) (Fig. 5), and a change in the abundance of species between sampling periods is therefore likely to change the *IndVal*s for the species concerned. For all species with abundance of approximately 630 individuals (log abundance = 2·8) or more, the fidelity value reached and remained at a maximum value of 1·0 (Fig. 5). The linear logistic model for the specificity
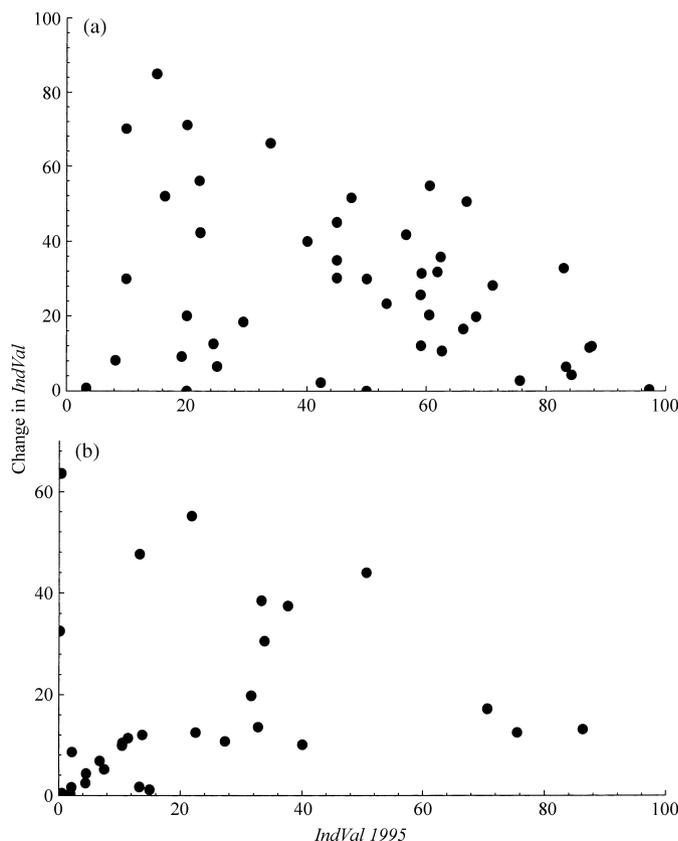
Fig. 3. Relationship between the indicator values (% *IndVal*) of species in the 1995–96 sampling period and the change in percentage *IndVal* for each species between this period and the 1998 sampling period for (a) mixed woodland ($F_{1,44} = 5.55$, $P = 0.02$, $R^2 = 0.15$) and (b) sand forest ($F_{1,29} = 0.53$, $P = 0.47$, $R^2 = 0.02$).
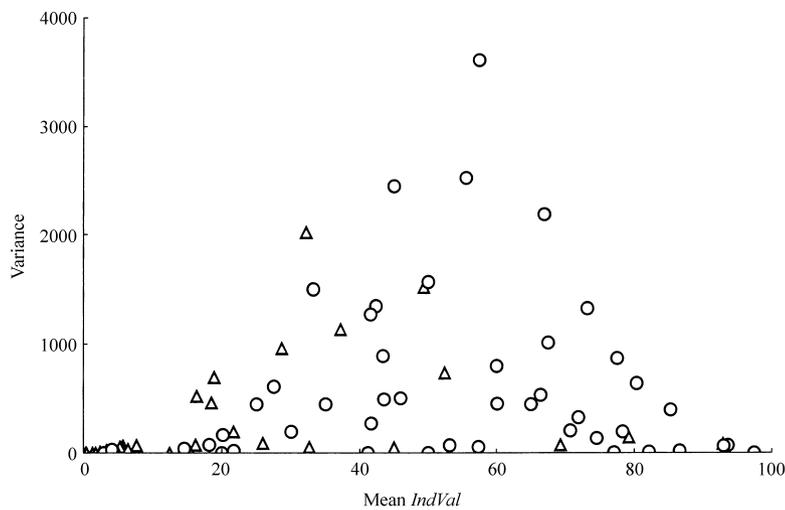
Fig. 4. Relationship between mean *IndVal*s and their variances across the two sampling periods for (circles) mixed woodland ($F_{1,44} = 0.05$, $P = 0.82$, $R^2 = 0.001$) and (diamonds) sand forest ($F_{1,29} = 2.69$, $P = 0.11$, $R^2 = 0.09$).

component of the *IndVal* was not significant (d.f. = 180, deviance = 140·79; abundance: d.f. = 1, $\chi^2 = 1.01$, $P = 0.32$), and specificity was therefore comparatively resistant to species abundance changes.

DETECTOR SPECIES

Eleven species met the detector selection criteria in the 1995–96 dung beetle assemblage (Table 3a). When

tested by including the disturbed sand forest assemblage in the *IndVal* analyses, five species responded as predicted, and four of these did so consistently across the two tests (Table 3b,c). Of these four species, two (*Onthophagus sugilatus* sp. A and *Onthophagus sugilatus* sp. C) may be regarded as characteristic of disturbed sand forest because their *IndVal*s were significant and greater than 70% for this habitat type. Species not predicted to be detectors were also analysed as in

Table 2. Percentage indicator values (significant *IndVal* > 70%) of Scarabaeidae species in two sampling periods (for species list see van Rensburg *et al.* 1999)

	%*IndVal* (April 1995 to May 1996)	%*IndVal* (December 1998)	70% criterion
Sand forest			
Sisyphus sp. Y *sensu* Paschalidis	86·32	99·47	>
Onthophagus lacustris	75·54	63·06	
Proagoderus aciculatus	70·64	87·82	=
Mixed woodland			
Sisyphus sordidus	97·23	97·66	>
Metacatharsius pseudopacus	87·61	99·50	>
Pedaria sp. III *sensu* Davis	87·24	98·73	>
Copris inhalatus prob. *sanctaeluciae*	84·26	80·00	>
Pedaria sp. IV *sensu* Davis	83·32	89·75	>
Kheper lamarcki	82·86	50·00	
Onthophagus ursinus	75·62	78·43	>
Euonthophagus carbonarius	71·08	99·32	=

70% criterion: >, species with *IndVal* significantly greater than 70% across two sampling periods (*t*-test, d.f. = 1, *P* < 0·05); =, species with *IndVal* not significantly different from 70% across two sampling periods (*t*-test, d.f. = 1, *P* > 0·05); unmarked species had a mean *IndVal* across the two sampling periods of < 70%.
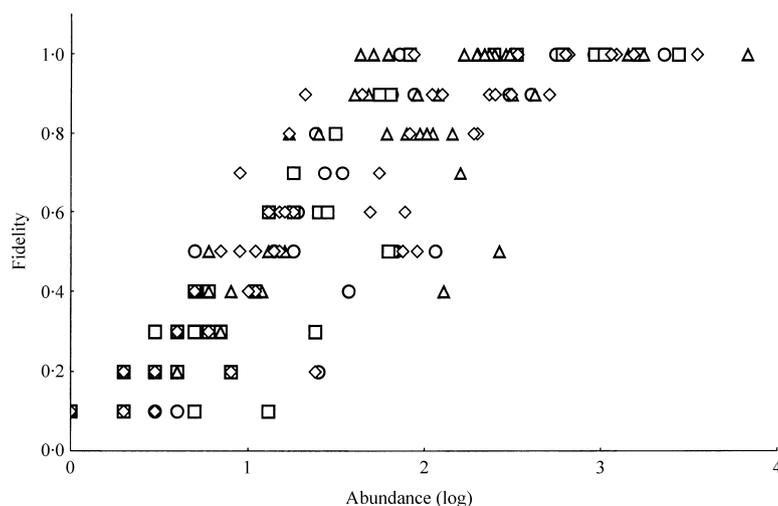
Fig. 5. Relationship between the fidelity component of the indicator value (*IndVal*) and the abundance (log$_{10}$) of species in mixed woodland and sand forest. Mixed woodland (mean fidelity ± SE): 1995–96 (diamonds) 0·61 ± 0·04 and 1998 (triangles) 0·66 ± 0·05. Sand forest: 1995–96 (squares) 0·46 ± 0·05 and 1998 (circles) 0·38 ± 0·06.

Table 3b,c, i.e. all species recorded in both 1995–96 and 1998 and not listed in Table 3a. None of these species responded as detectors. Therefore no potential detector species were missed in the initial detector species identification procedure (Table 3a).

Discussion

In this study a quantitatively predicted ecological bioindicator, in the form of a suite of dung beetle indicator species, was tested on an independent data set. Sets of species were found to be robust bioindicators, i.e. reliably characteristic across data sets of the habitat of which they were indicative. Furthermore, certain initially identified indicator species were discarded as unreliable and the suite of indicators was thus refined. This testing process improved the confidence with which the final suite of species may be

regarded as indicators. Further such testing will permit the calculation of confidence intervals for the indicator values of each species, whereby the reliability of these species as indicators will have been firmly established. As outlined previously, such reliability is essential to effective bioindication, and a testing process such as the one we outline here is thus advocated for all studies concerned with bioindicator identification (McGeoch 1998; Caro & O'Doherty 1999; Hilty & Merenlander 2000).

The indicator value method (Dufrêne & Legendre 1997) enabled the identification, as well as the testing, of these indicator species. Although the fidelity (frequency of occurrence) component of the *IndVal* measure provided by this method was shown to be sensitive to species abundance, the differences in abundance levels that occurred between the two studies did not obscure the identity of characteristic species.

Table 3. Indicator values (*IndVal* percentage) for dung beetle species predicted to be detectors. (a) Mixed woodland and sand forest data from 1995–96; (b) mixed woodland and undisturbed sand forest data from 1995–96 as well as disturbed sand forest data from 1998; (c) mixed woodland, undisturbed sand forest and disturbed sand forest data from 1998. Predictions were based on *IndVal*s from (a) (mixed woodland: $50 \leq IndVal < 70$; sand forest: $5 \leq IndVal < 50$) and tested using *IndVal*s in (b) and (c). Species in bold are characteristic species for disturbed sand forest (for species list see van Rensburg *et al.* 1999)

Data	Species	Mixed woodland	Sand forest	Disturbed sand forest	Difference in *IndVal*‡
(a)	1. *Catharsius tricornutus*	59·06*	13·75		
	2. *Onthophagus fimetarius*	61·89*	6·79		
	3. *Onthophagus* sp. near *vinctus*	62·39*	37·61		
	4. *Proagoderus dives*	68·37*	31·63		
	5. *Onthophagus* cf. *sugillatus* sp. A	66·23	33·77		
	6. *Onthophagus* cf. *sugilatus* sp. C	62·65	27·35		
	7. *Onthophagus stigmosus*	66·78	33·22		
	8. *Neosisyphus mirabilis*	60·61	21·82		
	9. *Pachylomerus femoralis*	60·51	32·76		
	10. *Copris puncticollis*	56·62	11·47		
	11. *Copris urus*	59·13	10·44		
(b)	1. *Catharsius tricornutus*†	46·10*	10·73	11·00	+0·27
	2. *Onthophagus fimetarius*†	44·32*	4·86	11·35	+6·49
	3. *Onthophagus vinctus*	53·79*	32·42	11·03	−21·39
	4. *Proagoderus dives*	66·82*	30·92	2·27	−28·02
	5. *Onthophagus* cf. *sugillatus* sp. A†	25·20	12·85	61·94*	+49·09
	6. **Onthophagus cf. sugillatus sp. C†**	12·98	5·67	**79·27***	+73·60
	7. *Onthophagus stigmosus*	65·66*	32·66	0·83	−31·83
	8. *Neosisyphus mirabilis*	60·60*	21·81	0·00	−21·81
	9. *Pachylomerus femoralis*	59·57*	32·25	0·93	−31·32
	10. *Copris puncticollis*	52·03*	10·54	2·43	−8·11
	11. *Copris urus*	56·67*	10·00	0·42	−9·58
(c)	1. *Catharsius tricornutus*†	72·00*	1·50	7·50	+6·00
	2. *Onthophagus fimetarius*†	2·61*	0	36·52	+36·52
	3. *Onthophagus vinctus*	29·78*	0·05	55·74	+55·69
	4. *Proagoderus dives*	86·85*	11·64	1·51	−10·13
	5. **Onthophagus cf. sugillatus sp. A†**	18·73	0·71	**77·83***	+77·12
	6. **Onthophagus cf. sugillatus sp. C†**	11·93	8·72	**77·06***	+68·34
	7. *Onthophagus stigmosus*	15·34	67·54*	2·89	−64·65
	8. *Neosisyphus mirabilis*	5·79	76·97*	0·00	−76·97
	9. *Pachylomerus femoralis*	78·35*	18·56	1·86	−16·70
	10. *Copris puncticollis*	89·86*	0·14	2·61	+2·47
	11. *Copris urus*	44·44*	0·56	0·56	0

*Indicator values (*IndVal*s) significant at $P < 0.05$.
†Species whose indicator values behaved as predicted.
‡This difference represents the percentage to which the species is a better (+) or worse (−) indicator of disturbed than undisturbed sand forest.
An *IndVal* of zero does not mean that the species was absent, merely that it has no indicator value in the context of the three habitats being compared.

Species with *IndVal*s of > 70% remained comparatively consistent between studies. We suggest three reasons why, in spite of the sensitivity of the fidelity value to species abundance, this is likely to be the case. First, as outlined earlier the fidelity value is calculated from relative, rather than absolute, differences in the frequency of occurrence of a species across habitats. As a result, if the abundance of a species changes in a similar direction across both habitat types this may not affect a change in its fidelity value. Second, the logistic nature of the relationship between fidelity and abundance (as well as the fact that abundance is logarithmic in the relationship) means that a substantial abundance change (over one order of magnitude) may not result in any change in fidelity. Third, there is likely to be some cross-compensation between fidelity and specificity

values. A decrease in the abundance of a species (and a resulting decrease in its fidelity value) may result in an increase in its specificity value if that value was initially less than the maximum of 1·0. Because frequency of occurrence and abundance are positively related, a decrease in one can result in a decrease in the other. If a species is present at fewer sites than it was originally, it may become apparently more habitat specific by disappearing from one or more habitats. This is particularly likely to be true of species with relatively high habitat specificity and low abundance in non-preferred habitats. A decrease in fidelity and increase in specificity value may, as a consequence, result in little or no change to the original *IndVal* for that species. Regardless of the mechanism, because of this resilience to change in abundance, which is an inherent characteristic

of species populations (Wolda 1988; Kingsolver 1989), the *IndVal* method has proven to be a particularly effective tool for ecological bioindication.

In addition to the method outlined for the identification of detector species using *IndVal*, empirical evidence was provided for detectors as a useful and complementary class of ecological bioindicator in this system. Detector species clearly demonstrated a change in habitat between two states, and, as predicted, were more prevalent (with higher *IndVal*s) in a habitat condition intermediate (i.e. disturbed sand forest) between the two habitat states than within the less preferred habitat state (i.e. undisturbed sand forest). Furthermore, they were indicative not only of this change in habitat state, but also of the direction of change. The latter information was obtained from the directional change (increase) in the prevalence of these species as the habitat changed from their less towards their more preferred habitat state.

Four species (one-third of the proposed total) were confirmed as detectors of a change in habitat from sand forest to mixed woodland, of which two were characteristic of disturbed sand forest. All four of these species were among the original suite of species predicted to be detectors. The method outlined for identifying detector species was thus effective. The shape of the relationship between the mean *IndVal* and its variance, however, suggests that, unlike characteristic species, the selection of detector species should not be based on average indicator values calculated from a temporal series of assemblage data. Whereas the variance (as well as between sampling period change) in the *IndVal* of characteristic species (*IndVal* > 70%) was shown to be low (change < 35%; Fig. 3), and their means are thus likely to be reliable predictors, the same was not true for species with *IndVal*s of between 30% and 70%. Because the *IndVal*, and thus its mean, is bounded between zero and 100, most mean *IndVal*s will lie closer to an intermediate *IndVal* of approximately 50% than the minimum or maximum *IndVal* from which they were calculated. Means based on very dissimilar values will also approach 50%, but will have high variances (a comparable phenomenon occurs in other bounded systems; Lyons & Willig 1997; Colwell & Lees 2000). Detector species by definition have intermediate *IndVal*s. Selection of detector species based on mean *IndVal*s across a number of sampling periods will therefore reduce the ability to discriminate between good detectors and species with highly variable *IndVal*s. Therefore close attention must be paid to the variance estimators of detector species, and only species within the necessary *IndVal* range and close to the abscissa of Fig. 4 will prove reliable.

Although no significant differences were found in average abundance or species richness between sand forest and disturbed sand forest, unique sets of indicator species were identified for each. These findings highlight the importance of a bioindicator-based approach to ecological monitoring, rather than the use

of a diversity index approach in which species identity plays no part (Cousins 1991). In addition, when using bioindicators, assessing change in sand forest using the full suite of indicator and detector species identified here is advisable. Not only do the indicator and detector species identified together have a higher information content than either group on its own, but more confidence can also be placed in the response of a suite of species than in any single species' response. The use of multiple rather than single species in bioindication has been advocated to minimize dependence on individual taxa and to improve confidence by basing conclusions on a wider array of responses (Hilty & Merenlander 2000).

Although the identities of indicator species were confirmed, species abundance differed markedly between the two studies. The December 1998 sample constituted one-twelfth of the sample effort of the 1995–96 study. However, the number of dung beetle individuals trapped were comparable to, and in some cases greater than in, the initial year-long study. None the less, it is particularly important that the assemblage data set for the year-long study be regarded as more representative than the December 1998 assemblage data, because it included the full spectrum of seasons and was thus not biased by interseasonal changes in species abundance (for a discussion see Davis 1997). Indeed, in terms of species richness it was more representative of the sand forest dung beetle assemblage than the 1998 sample. It is imperative that the initial selection of indicator species is based on temporally representative data, such as the 1995–96 data set, because dramatic inter- and intraseasonal changes in species activity and abundance may otherwise result in misrepresentation of indicator species. Species have been shown to undergo dramatic interannual abundance rank changes in dung beetle communities, their abundance fluctuates significantly between seasons, and they are highly sensitive to short-term fluctuations in weather conditions within seasons (Doube 1987). Therefore, species initially selected from a temporally representative data set are more likely to be robust indicators of a particular habitat type. Their high *IndVal*s are based on specificity and abundance values obtained for the spectrum of seasons and, in spite of inevitable abundance changes between seasons, these species remain specific to and abundant within the habitat of which they have been identified as indicative.

However, the financial and person-hour costs of obtaining representative data bases such as these are high (Noss 1990; Balmford, Jayasuriya & Green 1996; Spector & Forsyth 1998; Andersen *et al*. 2002). The same level of investment, although necessary initially, can seldom be maintained for ongoing longer-term monitoring of habitat integrity and change. Therefore, monitoring once a year during a peak activity period for the assemblage within which the bioindicators are found would dramatically reduce expenditure and improve the likelihood of support for a long-term

monitoring programme. Because the indicator species in this study compared favourably between the year-long study and the one conducted during a peak activity period, the study demonstrates that such an approach is feasible in this context, at least when dung beetles are the target ecological indicator.

Tembe Elephant Park contains the largest protected area of endangered sand forest and, as highlighted earlier, this habitat type is under severe pressure both inside and outside the Park. The information obtained and the conclusions drawn from this study will thus contribute to informed management of sand forest and mixed woodland in Tembe. The approach will also compliment existing botanical information on the effect of disturbance on sand forest and its associated biota (van Wyk 1996; van Rensburg *et al.* 2000a). Particular attention should be paid to disturbed sand forest inside and at the edges of the Park. For example, increasingly intense elephant foraging inside the Park results in an opening of the sand forest canopy, the effects of which may in some ways be similar to that caused by human occupation of sand forest outside the Park (van Rensburg *et al.* 1999). A tested suite of dung beetle indicators is now available for such monitoring within, and adjacent to, the Park.

Following a two-stage process when selecting bioindicators, i.e. quantitative identification and verification, will establish the degree of confidence with which they can be applied. This not only improves the efficiency of bioindication systems, but is likely to increase their successful adoption as management tools. Furthermore, paying particular attention to species with different combinations of specificity and fidelity values will maximize the information on habitat quality extracted from bioindicator assemblages.

Acknowledgements

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Appendix A

Dung beetle species first recorded in 1998 in sand forest and mixed woodland in Tembe Elephant Park, South Africa, and in disturbed sand forest outside the Park (for original species list see van Rensburg *et al*. 1999)

Species	Sand forest	Disturbed sand forest	Mixed woodland
Caccobius nigritulus Klug		×	×
Copris denticulatus Nguyen-Phung		×	
Copris sp. 1		×	
Gymnopleurus virens Erichson			×
Onthophagus bicavifrons d'Orbigny			×
Onthophagus cf. *sugillatus* sp. B		×	×
Onthophagus flavolimbatus Klug		×	×
Onthophagus lamelliger Gerstaecker		×	
Onthophagus pullus Roth	×	×	×
Onthophagus rasipennis d'Origny			×
Phalops flavocinctus Klug			×
Proagoderus brucei (Reiche)		×	
Sisyphus spinipes Thunberg	×		×