neric Nonindigenous Aquatic Organisms Risk Analysis Review Process recently updated in the United States (*28*), are based on expert opinion or qualitative assessments, and not on rigorously quantitative statistics. In contrast, the approach illustrated here is quantitative, repeatable, and transparent—characteristics a recent National Research Council report urges should apply to the next generation of risk assessments (*11*).

Although the results presented here are specific to the Great Lakes, this approach to constructing predictive models could be applied to a diversity of plant and animal taxa inhabiting a variety of terrestrial and aquatic ecosystems. As highlighted by the U.S. National Management Plan on invasive species (*5*), the urgent need to focus attention on prevention requires the development of species risk-assessment protocols. As alien species move along the invasion sequence (from transport to introduction, establishment, spread, and impact), management options become more limited. Even in the rare cases in which the knowledge and technology exist to control an established species, such efforts are expensive and must be practiced in perpetuity (*29*). For example, the United States and Canada jointly spend about U.S. $15 million annually to control sea lamprey (*Petromyzon marinus*) in the Great Lakes (*30*); these costs have been incurred since 1956 and will continue as long as sea lamprey control remains a management goal. Quantitative risk assessments that identify the alien species most likely to establish, spread quickly, and become a nuisance could be the foundation for efforts to prevent future expensive and environmentally damaging invasions.

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17. The reliability of our models (and all other models) is a function of the accuracy of the prediction and the frequency with which the event occurs at all (i.e., the "base rate," or proportion of introduced species that establish). Low base rate probability inflates the number of "false-positives" identified by the screening tool (species predicted to become established, spread quickly, or be perceived as a nuisance) (*31*). See online material for a discussion of the influence of base rate on our results.
18. CART was performed with CART software (Salford Systems, San Diego, CA).
19. Discriminant function coefficients for the spread DA (signs indicate association with spreading quickly): constant = 24.68635, survive higher temperatures = −1.52543, wide temperature range = 0.95508, closer to mature length by 2 years = −0.0000076.
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Supporting Online Material

www.sciencemag.org/cgi/content/full/298/5596/1233/DC1
Materials and Methods
SOM Text
Tables S1 to S9
References and Notes

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Avian Persistence in Fragmented Rainforest

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What factors determine the persistence of species in fragmented habitats? To address this question, we studied the relative impacts of forest deterioration and fragmentation on bird species in 12 rainforest fragments in Kenya, combining 6 years of individual capture-recapture data with measurements of current captures and museum specimens. Species mobility, as estimated from species-specific dispersal rates, and tolerance to habitat deterioration, as estimated from change in fluctuating asymmetry with increasing habitat disturbance, explained 88% of the variation in patch occupancy among eight forest bird species. Occupancy increased with mobility and with tolerance to deterioration, where both variables contributed equally to this relationship. We conclude that individual-level study, such as of dispersal behavior and phenotypic development, can predict patterns of persistence at the species level. More generally, for conservation tactics to stand a high chance of success, they should include action both within sites, to minimize habitat deterioration, and across landscapes, to maximize dispersal.

Anthropogenic habitat deterioration is imposing new selection pressures on organisms, increasing local extinction rates (*1*). Simultaneously, reduced movement among remnant patches lowers colonization rates, which further negatively affects demographic and genetic population parameters (*2*). From a conservation perspective, the impacts of habitat deterioration and the impacts of habitat fragmentation might demand different strategies. Whereas the former often requires management of populations within local (protected)

Table 1. Species-specific dispersal probabilities as estimated with recapture rates and multistrata models fitted in MARK.

Species	Recapture rate*	Model	Dispersal probability,Ψ	Model†	Dispersal probability,Ψ‡
A. milanjensis	0.083	$\Phi_g p_c \Psi_c$	0.002535	$\Phi_g p_c \Psi_g$	0.005994
N. olivacea	0.114	$\Phi_g p_c \Psi_c$	0.003958	$\Phi_g p_c \Psi_g$	0.007775
P. cabanisi	0.077	$\Phi_g p_c \Psi_c$ $\Phi_g p_g \Psi_c$	0.002161§ 0.002102	$\Phi_g p_g \Psi_g$	0.001998
P. ruficapillus	0.000	$\Phi_g p_c \Psi_c$	0.000000	$\Phi_g p_c \Psi_g$	0.000000
P. stellata	0.024	$\Phi_g p_g \Psi_c$	0.000761	$\Phi_g p_g \Psi_g$	0.001881
T. helleri	0.006	$\Phi_g p_g \Psi_c$	0.000184	$\Phi_g p_c \Psi_g$	0.000132
Z. silvanus	0.079	$\Phi_c p_c \Psi_c$	0.003080	$\Phi_g p_c \Psi_g$	0.006849

*Calculated as the proportion of all recaptured birds that moved between the three large fragments. †Multistrata model that estimates dispersal probabilities between pairs of fragments irrespective of the direction of dispersal. ‡Species-specific probability of dispersal, controlling for dispersal distance (see text for details). These estimates were used for further modeling. §For *P. cabanisi*, two models were equally parsimonious. The Ψ estimated from the model with the lowest AIC value was selected for further analysis.

areas, the latter may require conservation at the landscape level, within a metapopulation framework (*3*).

We evaluated the impact of habitat deterioration and fragmentation on the persistence of eight forest-restricted small- to medium-sized bird species within 430 ha of rainforest remnants in southeast Kenya. Three species are endemic to the Taita Hills forest, which is part of the Eastern Arc biodiversity hotspot (*4*). Over the past decades, the forest has been reduced to 12 patches, of which only the three largest ones (Chawia, 94 ha; Ngangao, 136 ha; and Mbololo, 179 ha) are inhabited by all study species. The nine other remnants are tiny (1 to 8 ha) and heavily disturbed, and they host breeding populations of a subset of species only (*5*). At a landscape level, pronounced heterogeneity in habitat quality, such as among the Taita forest fragments, may give rise to source-sink dynamics within a metapopulation (*6*). From metapopulation theory, we hypothesized occupancy of the smaller forest patches (*7*) to be a function of both species-specific levels of mobility, affecting (re)colonization rates from the three large patches, and sensitivity to forest deterioration, affecting local extinction rates.

Species-specific levels of mobility were estimated with the program MARK (*8*) from capture-recapture histories of 3089 individuals trapped and individually marked in the large fragments Chawia, Ngangao, and Mbololo between 1996 and 2002 (*9*). Monthly probabilities of between-fragment dispersal were estimated from multistrata mark-recapture models and corrected for between-species heterogeneity in survival and/or recapture rates (*10*). Initially, we estimated species-specific rates of dispersal by assuming a constant dispersal probability for each species. This resulted in four candidate models: (i) $\Phi_g p_g \Psi_c$, (ii) $\Phi_c p_g \Psi_c$, (iii) $\Phi_g p_c \Psi_c$, and (iv) $\Phi_c p_c \Psi_c$, where Φ is the monthly survival probability, p is the monthly recapture probability, Ψ is the monthly dispersal probability, and the subscripts g and c refer to fragment-dependent or constant probabilities, respectively. From these models, the most parsimonious one was selected for each species. However, because distances differed between pairs of fragments (Mbololo to Ngangao, 11.3 km; Mbololo to Chawia, 19.4 km; Ngangao to Chawia, 10.9 km), estimates of dispersal might be biased by differences in abundance between fragments for the different species. We therefore constructed multistrata models that estimated monthly dispersal probabilities between each pair of fragments irrespective of the direction of dispersal, by allowing Ψ to vary between fragment pairs (*11*). The process of selecting the most parsimonious model among the new candidate set was then repeated for each species. In a final step, we regressed pairwise dispersal probabilities against pairwise distances between the three forest fragments for each species, then used the intercept of each regression equation as the species-specific measure of dispersal (mobility) for further modeling. The multistrata models and dispersal probabilities estimated for each species are listed in Table 1. All methods of estimating species-specific dispersal produced comparable between-species differences in mobility.

Species-specific levels of stress tolerance were estimated from levels of fluctuating asymmetry (FA) in tarsus length. FA refers to small, nondirectional differences in the development of the left and right sides of bilateral traits (*12*) and is widely regarded as a measure of developmental stability and a predictor of stress-mediated changes in fitness (*13*). Individual FA estimates were based on repeated measurements, corrected for body size, and obtained from mixed model analysis with restricted maximum likelihood parameter estimation to distinguish FA from directional asymmetry and measurement error (*14*). We previously showed a consistent, positive relationship between current population levels of tarsus FA and the degree of forest deterioration (*15*, *16*). We further measured tarsus FA in 133 museum specimens of six study species that were collected before the majority of the Taita Hills forest patches became severely deteriorated several decades ago (*17*). Sensitivity to forest deterioration was calculated as the species-specific deviance from the average increase in tarsus FA between museum samples and current captures in the most degraded of the larger fragments (Chawia), relative to a control patch with the most intact indigenous vegetation (Mbololo) (*18*). Previous analyses confirmed that levels of

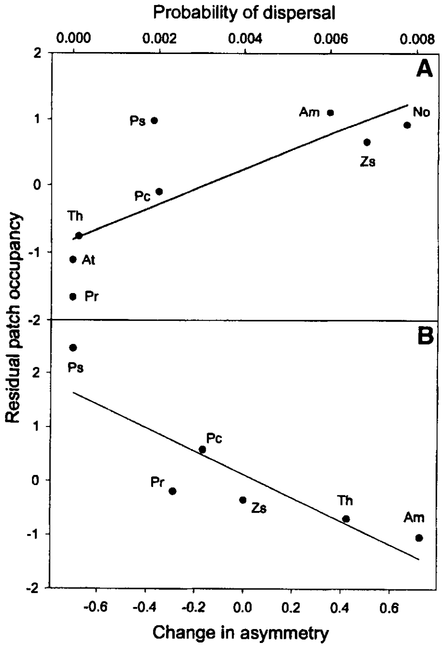

Fig. 1. Relationship between persistence and species-specific levels of (**A**) mobility and (**B**) stress tolerance. Ordinates represent residual values of patch occupancy (*7*) after (A) correction for the effects of change in asymmetry and (B) correction for dispersal rate. Patch occupancy was positively related to dispersal rate (parameter estimate 301 ± 111, 95% CI 94 to 532) and negatively related to change in asymmetry (shown in millimeters, parameter estimate −1.87 ± 0.74, 95% CI −3.39 to −0.50). Parameter estimates of the two variables were not statistically correlated ($P = 0.3$) and remained unaffected after variable body size was included in the model. Am, *Andropadus milanjensis* (3 small forest fragments occupied, $n_{tot} = 9$); At, *Apalis thoracica* (1); No, *Nectarinia olivacea* (7); Pc, *Phyllastrephus cabanisi* (4); Pr, *Phylloscopus ruficapillus* (0); Ps, *Pogonocichla stellata* (8); Th, *Turdus helleri* (1); Zs, *Zosterops silvanus* (5).

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FA increased over time in the degraded patch but not in the control patch (*15*).

More mobile species showed a significantly higher level of persistence than less mobile species after correction for the effects of change in asymmetry, i.e., they occupied a higher proportion of patches than expected from their estimated stress sensitivity (Fig. 1A). Highly comparable results (*19*) were obtained when we used the estimates of recapture rate and constant dispersal probability listed in Table 1. Change in asymmetry, in turn, significantly explained residual variance in patch occupancy (Fig. 1B), i.e., less sensitive species occupied a higher proportion of patches than predicted from their estimated level of mobility (*20*). Together, dispersal rate and change in asymmetry explained 88% of the observed variation in patch occupancy between species, with each factor contributing equally to the relationship (45% of the variation was explained by probability of dispersal; 43% of the variation was explained by change in asymmetry).

On the basis of these results, we conclude that individual-level parameters, such as mobility and developmental homeostasis, can be scaled up to predict species-specific patterns at landscape level [the "behavioral ecology of ecological landscapes" concept (*21*)]. In a comparable approach, models have been developed that scale mass-related energy requirements with population density (*22*). The use of simple, accurate, and cost-effective biomarkers, such as individual asymmetry, further permits us to measure the impact of environmental stress and to take appropriate conservation action before species become irreversibly affected [the "early warning" concept (*23*, *24*)]. Application of such an individual-level approach, in part of one of the world's most threatened biodiversity hotspots, suggests that conservation tactics may fail unless they include action both within sites, to minimize habitat deterioration, and across landscapes, to maximize dispersal.

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10. We used Akaike's Information Criteria (AIC) to determine the most parsimonious model among a candidate set and computed species-specific dispersal probabilities for further analysis from this model. Recapture data were too sparse to include fully time-dependent models of survival and recapture probabilities in the candidate set of models, and sample size did not allow us to calculate complex multistrata models for *Apalis thoracica*. For this species, no single individual was captured in more than one fragment, hence Ψ was estimated as 0. There is no formal goodness-of-fit test for multistrata models, yet our results were robust for a range of 1 to 1.5 in the overdispersion parameter $\hat{c}$.
11. More complex dispersal models could not be fitted to all species in MARK because models were overparameterized. For the more mobile species with adequate numbers of recaptures after dispersal between fragments, a model assuming direction-dependent dispersal rates between fragment pairs fitted the recapture data significantly better than the direction-independent model described in Table 1 for two species, but equally as well as the direction-independent model for two other species (nested models were compared using likelihood ratio tests).
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The Control of Spikelet Meristem Identity by the *branched silkless1* Gene in Maize

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Most of the world's food supply is derived from cereal grains that are borne in a unique structure called the spikelet, the fundamental unit of inflorescence architecture in all grasses. *branched silkless1* (*bd1*) is a maize mutation that alters the identity of the spikelet meristem, causing indeterminate branches to form in place of spikelets. We show that *bd1* encodes a putative ERF transcription factor that is conserved in different grasses and is expressed in a distinct domain of the spikelet meristem. Its expression pattern suggests that signaling pathways regulate meristem identity from lateral domains of the spikelet meristem.

Development in plants depends primarily on the activity of meristems, indeterminate cell populations whose derivatives form lateral organs. Meristems can be considered determinate or indeterminate, depending on whether they are consumed in the production of lateral primordia. Grass species have evolved unique meristem fates that are central to orchestrating the diverse inflorescence architecture found in this extensive family (*1*, *2*).

Both the male and female inflorescence meristems of maize (tassel and ear, respectively) produce spikelet meristems, determinate branches that produce two glumes and two florets before undergoing sexual specialization (*2*). *bd1* mutants show a loss of determinacy in the maize ear,