

The Metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms

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Dispersal of organisms generates gene flow between populations. Identifying factors that influence dispersal will help predict how species will cope with rapid environmental change. We developed an innovative infrastructure, the Metatron, composed of 48 interconnected patches, designed for the study of terrestrial organism movement as a model for dispersal. Corridors between patches can be flexibly open or closed. Temperature, humidity and illuminance can be independently controlled within each patch. The modularity and adaptability of the Metatron provide the opportunity for robust experimental design for the study of 'meta-systems'. We describe a pilot experiment on populations of the butterfly *Pieris brassicae* and the lizard *Zootoca vivipara* in the Metatron. Both species survived and showed both disperser and resident phenotypes. The Metatron offers the opportunity to test theoretical models in spatial ecology.

Space plays a pivotal role in the understanding of most evolutionary and ecological processes¹. Dispersal behavior—that is, the way individuals move across landscapes and induce gene flow among populations²—is a focal theme in spatial ecology. Identifying which ecological and evolutionary factors shape dispersal is critical for the understanding of how species will cope with shifting environmental conditions associated with global climate changes and habitat destruction³⁻⁵. Knowing the speed and magnitude of changes in species distribution ranges will help to anticipate the dislocation of ecosystems and ecosystem services⁶.

Studying dispersal requires a good understanding of its three basic stages: emigration (decision to leave a habitat), transfer (movement across often unviable habitats) and immigration (settlement in a new habitat). These three stages can be modulated

by the same or by different factors, with dispersal being the result of interaction between all influencing factors at each stage of the process⁵.

Dispersal studies were hitherto mainly restricted to the observation and modeling of natural systems, without the possibility of experimentally validating the resulting predictions. Many studies of dispersal and global warming have been performed (some are ongoing) using replicates of natural fragmented landscapes at various spatial scales, from patches of mosses (on a scale of decimeters squared) to forest ecosystems (on a scale of hectares)⁷⁻¹². Among them, the Savannah River Site Corridor Experiment considers eight replicates of patchy landscapes to study dispersal in terrestrial organisms with an emphasis on the role of ecological corridors in the maintenance of biodiversity⁹⁻¹¹. However, none of these studies provided control over spatial configurations and other relevant factors involved in the dispersal response, such as climatic conditions or population densities. Most experimental arenas dedicated to dispersal studies that allow full control of drivers are laboratory microcosms, a setup that restricts the choice of biological models to small organisms¹³⁻¹⁵. Experimental systems are needed that allow a direct validation of dispersal-related predictions at a more appropriate spatial scale. Outdoor experimental arenas for studying dispersal in lizards¹⁶⁻¹⁸ and mammals¹⁹ have been developed; however, these systems are not easily adaptable to other organisms, lack control over environmental parameters and are limited in the number of species and experimental units and in the size of the arenas.

We therefore developed the Metatron, a unique experimental infrastructure composed of 48 interconnected patches. The Metatron can host a broad set of terrestrial organisms and is dedicated to the study of dispersal within metapopulations²⁰,

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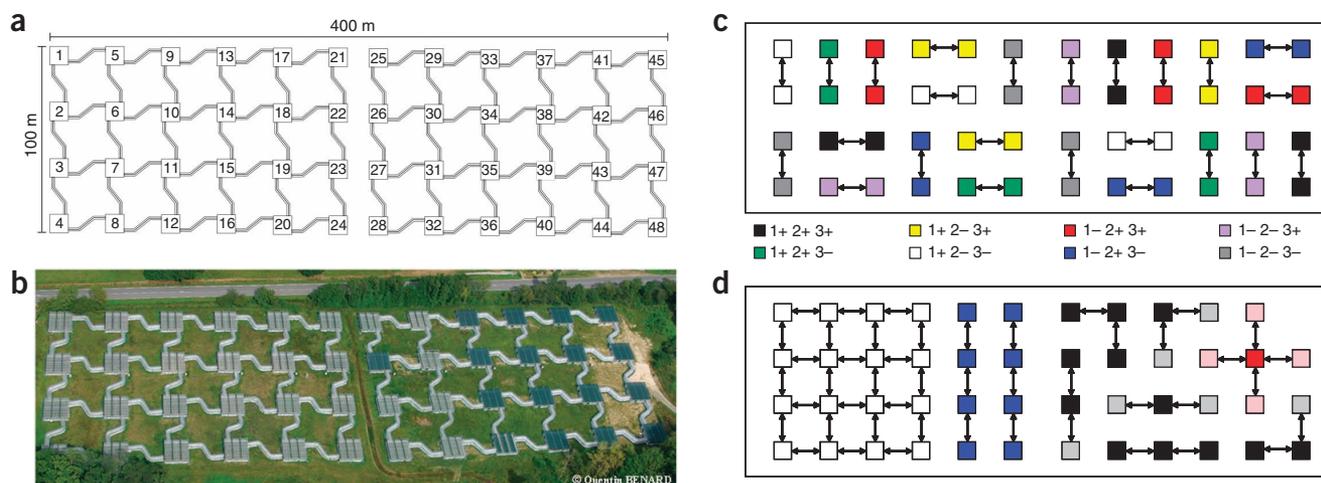


Figure 1 | Layout of the Metatron. (a) Spatial arrangement of the Metatron. Two sets of 24 patches installed in a 6×4 configuration (1–24 and 25–48) have been constructed on a 4-ha parcel. (b) Aerial photograph of the Metatron. On the right, shutters are closed on the top of 17 patches. (c) Example of experimental design with three factors (1–3) with binary states (such as presence/absence) in three replicates. The eight possible combinations are in different colors. Spatial arrangement of replicates is random. (d) Examples of simultaneous complex experimental designs. White, two-dimensional stepping stones; blue, two replicates of linear stepping stones; black and gray, two replicates of three connected patches in which individuals of the central population have the choice to disperse into empty patches (gray), into one occupied and one empty patch, or into two occupied patches (black); red, starlike configuration in which individuals of the central population have the choice to disperse in all directions into empty patches (pale red).

metacommunities²¹ and metaecosystems²². It offers experimental control of spatial and climatic factors in semi-natural conditions and thus aims at filling the gap between studies in natural systems and experiments in small microcosms. The Metatron is an open-access infrastructure run by the Analysis and Experimentation on Ecosystems Services (ANAEES) ANR program. The procedure for research groups to gain access to the Metatron (**Supplementary Note**) is described at <http://www.ecoex-moulis.cnrs.fr/experimental-platform/article/procedure-to-access-the-metatron/>. The Metatron will be useful to address key issues in the field of global change ecology.

RESULTS

The Metatron

We developed an infrastructure composed of 48 interconnected caged patches located on 4 ha of land (**Fig. 1a,b**). This allows up to three replicates in an experimental design involving three factors and their interactions in complex spatial configurations (**Fig. 1c,d**). The volume of a patch is 200 m^3 ($10 \text{ m} \times 10 \text{ m} \times 2 \text{ m}$), and patches are connected to their neighbors by 19-m-long corridors (**Fig. 2a**). The structure is covered with insect-proof nets (mesh = $920 \mu\text{m}$) and enclosed with a solid plastic base buried 0.5 m deep to restrict movement of individuals below the ground. The quality of patches can be manipulated according to the experimental design by planting selected species, pruning the vegetation or installing rocks or other obstacles.

The quality of corridors will also depend on experimental design. In natural situations, the quality of linkages between populations ranges from completely hostile environments to more favorable environments. We developed corridors that mimic unfavorable habitats that are challenging to cross in order to discriminate between dispersal and resident phenotypes. Alternatively, corridor habitat quality could equal the patch habitat quality, simulating ‘ecological corridors’.

Corridor entries represent less than 2% of the total vertical surface area of patches, and illumination is lower and temperature is higher in corridors than in patches. Vegetation height and structure can be manipulated to change corridor ‘viscosity’ (resistance to the movement of dispersing individuals). Corridors can be opened or closed between selected patches, and the entries can be split into two on the basis of height to favor dispersal of flying or ground-dwelling organisms (**Fig. 2b**). Corridors are divided lengthwise, which allows bidirectional monitoring of movements¹⁶ (**Fig. 2a–c**).

For example: consider two patches, A and B, connected by a twin system composed of corridors 1a and 1b. When corridor 1a is open and corridor 1b is closed in patch A while corridor 1a is closed and corridor 1b is open in patch B, only one-way movements are allowed (from patch A to B via corridor 1a, from patch B to A via corridor 1b). It is then possible to precisely monitor the number of emigrants from a given patch moving into each connected target patch, either by trapping individuals at the extremities of corridors (**Fig. 2c**) or by recording their movement with tags (automatic devices using individual radio-frequency identification chips). Corridors in the Metatron have two linear sections angled at the center (**Fig. 2d**), a configuration that prevents an animal from seeing the neighboring patch at the time of the emigration decision and until it is halfway through the corridor.

Within patches, natural ground-vegetation microhabitats specific to the chosen model organism can be recreated (**Fig. 2e**). At the patch center, standard sensors routinely record temperature, humidity and illuminance; additional sensors can be added on demand. Continuous records are automatically compiled by the TAC Vista program (Tour Andover Controls and Schneider Electric), an application specifically developed for the Metatron (**Fig. 3**). Microclimatic conditions within each patch differ slightly from external conditions because of the greenhouse effect associated with patch enclosure. Between July and December 2010,

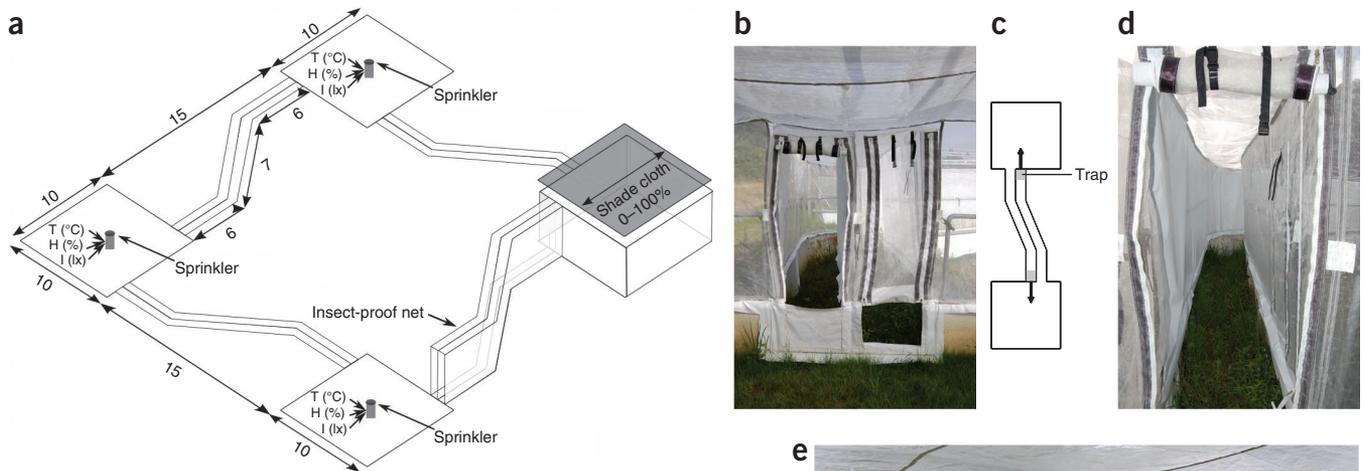


Figure 2 | Description of patches and corridors. **(a)** Layout of four patches of the Metatron. Sprinklers and sensors recording temperature (T), humidity (H) and illuminance (I) are at the centers of the patches. The lower-right patch is represented with total enclosure of its roof. Dimensions are in meters. **(b)** Corridor entries showing the twin system. The left corridor is opened to favor flying-animal crossings; the right corridor is opened to favor nonflying-animal crossings. **(c)** Schematic showing trap configuration in twin corridors (these may be pitfall traps or insect or bird nets, depending on the needs of the experiment). Arrows indicate the release of trapped individuals in the arrival patch. **(d)** Interior of a corridor showing the beginning of the central elbow. **(e)** Interior of a patch. Artificial elements (flower pots, thermoregulation sites in wood and rocks) provide microhabitat heterogeneity and can be designed to provide resources mimicking the natural habitat. The sensors and sprinkler are protected with plastic and labeled with the patch identification number.

inside mean temperature was on average 0.82 °C higher than outside mean temperature (*F* test, *P* = 0.05, **Fig. 4**). Motor-driven shutters above the patches can be automatically opened or closed from 0 to 100% on each side of the roof to generate shade (**Figs. 1b** and **2a**). Intermediate closure of these shutters creates heterogeneous climatic conditions both between and within patches.

Rotating sprinklers placed at the center of patches simulate rainfall or allow moisture to increase the air and soil humidity (**Fig. 2a,e**). The shutter and sprinkler systems can be independently activated within patches for predefined time intervals. Patch-specific temperature and illuminance instructions drive the activation of the shutter system, and humidity instructions activate the sprinkler

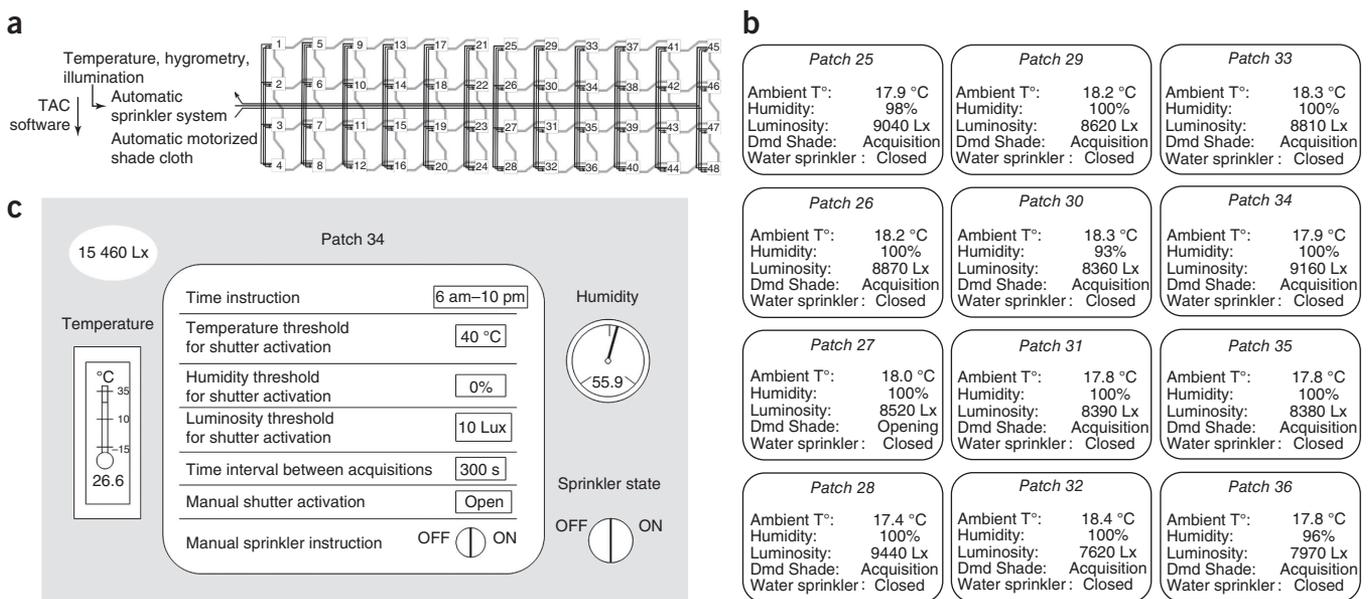


Figure 3 | Measurement and control of climate parameters. **(a)** Representation of the network allowing data acquisition and parameter control via the TAC Vista application. **(b)** Representation of the user interface of the TAC Vista application. Parameters of each patch are represented in a single white box. Dmd Shade parameter means ‘demand for shade’. Twelve patches are shown here. **(c)** Representation of the instructions for a target patch.



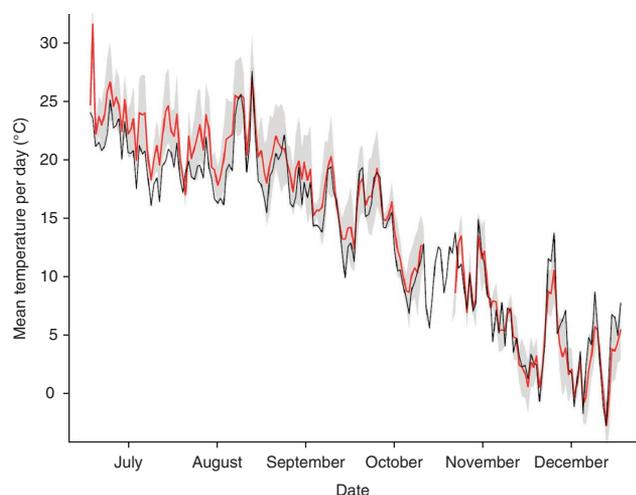


Figure 4 | Temperature within patches. The graph shows mean daily temperature over 24 patches of the Metatron from July to December 2010 (red) with confidence intervals (gray). The black curve represents outside mean temperature. Records were not available at some time points (between October and November) because of technical maintenance.

system. Automated instructions can be programmed through TAC Vista (**Fig. 3b,c**). This integrated system permits the creation of environmental gradients; continuous recording within each patch provides for a feedback control of the artificial climate (**Fig. 5**).

Survival, dispersal and metapopulation dynamics

We studied two biological models in the Metatron, conducting preliminary tests aimed at determining survival and dispersal tendencies. We mimicked classic metapopulations, defined as groups of local populations in which the movements of individuals between habitat patches is possible²⁰, using high-quality patches with resources (food, water, shelter and host plants), and inhospitable corridors.

The common lizard (*Z. vivipara*) is a small lacertid inhabiting humid habitats in Eurasia. In August 2010, we released 208 females and 131 males into 14 patches of the Metatron, with each patch connected to two other patches (an empty and another occupied patch). Dispersal movements were monitored by checking traps at the end of each corridor daily (Online Methods) from August to

October and from March to April (winter months were excluded because of hibernation). In total, 72 individuals (21%) crossed a corridor at least once. Among these, 34 individuals crossed a corridor a second time (47%). In June 2011, all surviving lizards were recaptured and kept in the laboratory until the females gave birth. Yearly survival probability in this experiment was 0.49 for both females and males; 23 females and 14 males were captured in previously empty patches, and populations in 2 of the 14 patches became extinct. Of the 102 recaptured females, 72 were gravid. Clutch size was 6 ± 0.24 s.d. and the proportion of live hatchlings within clutches was $81 \pm 3\%$ s.d.

In lizards, survival rates in natural conditions vary between recently translocated individuals, defined as individuals recently added to natural populations (adult females: 0.31, adult males: 0.21), and resident individuals, defined as individuals originally from natural populations (adult females: 0.70, adult males: 0.51)²³. In the Metatron, adult survival rates were much higher than those of recently translocated individuals in the wild but lower than those of resident individuals in the wild. Dispersal rates, clutch size and clutch success 1 year after the start of the experiment were similar to those observed in natural populations²³.

The large white butterfly (*P. brassicae*) is a nomadic butterfly with a 1-month generation time. Adults constantly explore their environment to acquire the resources they need, and dispersal may occur any time in an individual's life²⁴. We released 211 butterflies over four sessions within eight patches of the Metatron, with each patch connected to another empty patch, and left individuals in the system until death. The position of each butterfly was recorded by daily capture sessions, and each butterfly was released at its capture position after identification. Daily capture probability was equivalent between sessions and different between sexes: 0.82 for females and 0.75 for males. In contrast, survival probability was not dependent upon sex, but it varied between capture sessions. Lifespan varied between 1 and 21 d for females (mean \pm s.d. = 7.35 ± 3.99 d) and between 1 and 14 d for males (mean \pm s.d. = 6.28 ± 3.28 d). Survival was dependent on the age at release in both males ($n = 98$, $P < 0.001$, $R^2 = 0.1027$) and females ($n = 113$, $P < 0.001$, $R^2 = 0.1329$). Less than 15% of the total variance in the minimal survival of both sexes was due to the time spent in the laboratory before release. In butterflies, reliable information about fitness in natural conditions is not available. A comparison between survival

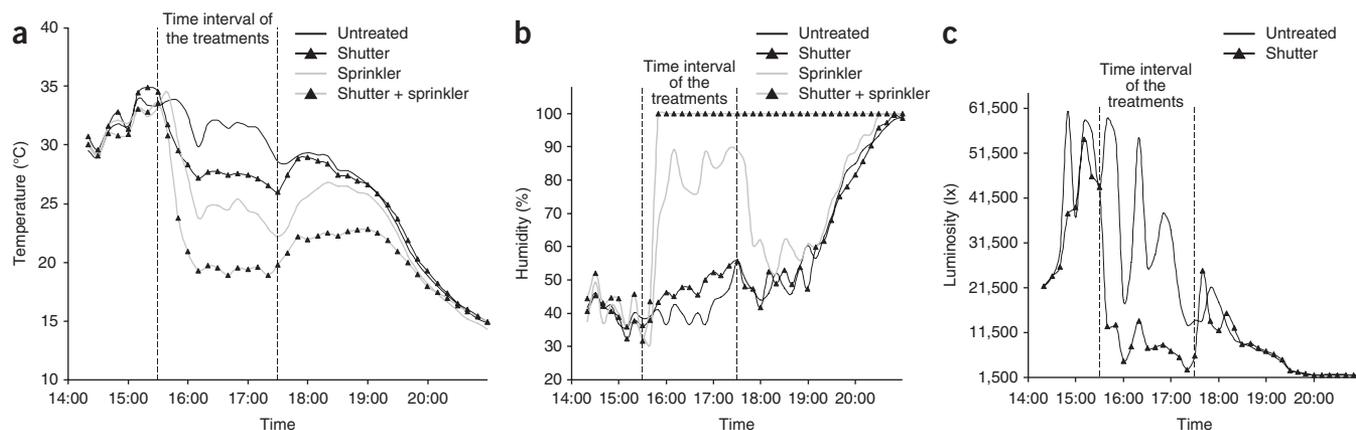


Figure 5 | Impact of the shutter and sprinkler systems on climatic conditions within patches. Four different conditions were applied in test patches for 2 h on 28 August 2011: total enclosure of the shutter, sprinkler activation, total enclosure of the shutter plus sprinkler activation, and no treatment. (a–c) The records of temperature (a), humidity (b) and illuminance (c) over 7 h are shown. The time interval of treatments is indicated in each case.

in the Metatron and in the laboratory revealed that outdoor conditions in the Metatron were less favorable than fully controlled laboratory conditions with 14:10-h light:dark cycles at 23 ± 1 °C (female survival in the laboratory = 18.65 ± 0.17 d, $n = 2,807$ and 16.43 ± 0.18 d for males, $n = 2,952$; error in s.d.).

Among the 178 recaptured butterflies (83 males, 95 females), 50 individuals (14 males, 36 females, 28% total) crossed a corridor at least once, which is in the range of dispersal rates in natural metapopulations²⁵. After release, we verified that butterflies showed natural behaviors: they explored the initial patches, flew, fed, and chased conspecifics. Dispersers (defined as individuals that crossed a corridor at least once) were present in each of the eight replicates. Among these, 52% performed at least two successive crossings (9 males, 17 females). Females laid 43 egg clutches, of which 5 were laid in previously empty patches by dispersers. In total, 229 butterflies were recruited from the clutches, of which 8 originated from previously empty patches. Three out of the eight populations became extinct at the next generation.

DISCUSSION

We present a unique infrastructure, the Metatron, to study dispersal in a wide range of species in controlled semi-natural conditions. The Metatron offers the possibility of imposing warmer-than-ambient conditions and of creating environmental gradients to test how climate changes may impact organism mobility. Unlike natural systems, the Metatron provides data on interpatch movements of a large number of individuals during their entire lifetime. Populations can be established within large habitat patches connected by unfavorable habitats, both in terms of size and environmental conditions, within which all individual movements can be recorded at an unexplored spatial scale. The spatial arrangement of the patches and the modularity of the corridors allow users to perform experiments according to various population models, including stepping stones.

In our pilot studies, we could distinguish ‘residents’ (those individuals that stayed in the same patch during the entire experiment) and ‘dispersers’ (those individuals that crossed corridors and moved from one patch to another). We have further observed that individuals inclined to each strategy were also characterized by a suite of other phenotypic traits, including flying performance and sex in butterflies (D.L. *et al.*, unpublished data) and body size, ventral coloration and behavioral traits in lizards (J. Cote and J. Clobert, unpublished data). We recorded U-turn behavior of butterflies entering the corridors and immediately returning to the patch. Such 180° changes in flight direction at the edge of favorable patches have been described as reluctance to leave suitable habitat patches in natural populations and are characteristic of resident phenotypes^{25,26}.

We believe that movement between patches in the Metatron can serve as a model for dispersal in natural conditions. First, as in natural conditions, we observed different dispersal phenotypes. Second, the Metatron successfully mimics the three basic stages of dispersal. As such, experiments aimed at studying the effect of density, sex ratio or habitat quality on dispersal decision can be established in the Metatron. Experiments dealing with informed dispersal (dispersal decision based on information provided by immigrants regarding alternate habitat⁵) may also be effectively undertaken. Third, successive crossings between patches, extinctions of populations and the settlement of individuals

and their subsequent reproduction in initially empty patches indicate that the Metatron can be used to study colonization dynamics. In both a long- and a short-lifecycle species, and in a flying and nonflying species, reproductive events were observed in occupied and colonized patches. We thus speculate that the system should be useful for studying long-term metapopulation dynamics²⁷ for a range of organisms.

If the appropriate vegetation and microhabitat are provided, the Metatron is suitable for studying a range of terrestrial organisms including terrestrial plants, molluscs, arthropods, reptiles and small mammals, as well as some amphibians and some semi-aquatic species. It should also offer the possibility of observing between-species interactions such as predator-prey interactions or interspecific competition for space or resources, opening interesting perspectives to study metacommunities. Promising applications include studying the impact of global changes on the temporal and spatial asynchrony between predators and prey, disentangling the effects of intra- and interspecific diversity on the movements between communities, and testing for connectivity effects on species interaction. Finally, the Metatron enables the reconstruction of complex ecosystems in specific patches and the option to add new automatic sensors (such as for pH, redox potential or nutrient concentrations) to evaluate flows of energy and material, in addition to flows of individuals, for the study of metaecosystems. Studying the ability of ecosystems to recover stable states after perturbations would be of particular interest in the context of increasing anthropogenic pressures.

Nevertheless, some limitations must be considered, and results obtained in the Metatron should be extrapolated to natural systems with caution. First, the Metatron patch size may not be representative of the natural patch size for many species, although we note that previous studies have demonstrated that local patterns of dispersal can be scaled up to reveal larger-scale patterns^{10,28}. Second, the enclosure of the patches implies that the population dynamics expected in the Metatron may be different from those in natural systems. Indeed, (i) population sizes are constrained, which can lead to more frequent extinction-recolonization events, and (ii) populations evolve within closed environments. Rather than being purely limiting, however, these two features also offer exciting perspectives for conservation biology, which deals precisely with the problems associated with restricted population sizes and directional selection. Third, the narrow and relatively short corridors are not representative of the connectivity of many natural systems. Complete duplication of real dispersal distances of medium-sized organisms, varying from a few meters to tens of kilometers, is obviously impossible. The Metatron, however, trades off dispersal distance against corridor viscosity. Particularly hostile corridors will lead to situations in which individuals in the transfer phase of the dispersal process will be confronted with highly challenging situations, just as individuals dispersing in a natural highly fragmented landscape. This distance-viscosity trade-off must be considered before applying the results to natural systems.

The Metatron paves the way for significant knowledge breakthroughs in spatial ecology, provided that extrapolations to natural systems are carefully weighted according to the Metatron's inherent constraints. This system should enable experimental validation of concepts describing the movement of organisms between spatially separated habitats and the environmental factors affecting these movements. This is a crucial and timely issue,

as insights from these theories influence biodiversity conservation in the face of the destruction of natural habitats and its interaction with climatic change. The Metatron offers ecologists the possibility of conceiving robust experimental designs aimed at testing hypotheses at a new spatial scale, and thus of validating currently untested predictive models.

METHODS

Methods and any associated references are available in the online version of the paper.

Note: Supplementary information is available in the online version of the paper.

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AUTHOR CONTRIBUTIONS

J. Clobert had the initial idea and managed the fund acquisition for the construction of the Metatron. J. Clobert, J.L., J.-F.L.G., O.G., Q.B. and M.B. participated in the final conception of the system, and J. Clobert, O.G. and Q.B. solved all the technical issues. D.L., A.T., O.C. and M.B. collected butterfly data. J. Cote, F.Z., S.Z., O.C. and J. Clobert collected lizard data. D.L. and A.T. analyzed the butterfly data. J. Cote analyzed the lizard data. D.L., O.G., M.B., J. Cote, J.-F.L.G. and J. Clobert wrote the paper. All authors commented on and approved the final version of the paper.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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ONLINE METHODS

Lizard experiment. In July 2010, 208 female and 131 male lizards were captured in the Cevennes (Mont Lozère, South of France, 44°27'N, 3°44'E) and brought to field station of Moulis (Centre National de la Recherche Scientifique, Ariège, France). Individuals were individually marked and kept in the laboratory. To provide each individual with the same standardized environment (for example: food, water, heat and social interactions), lizards were individually housed in plastic terrariums with a 3-cm litter layer. In one corner of the terrarium, a bulb provided heat for thermoregulation and light from 9:00 to 12:00 and from 13:00 to 17:00. A piece of cardboard and a plastic tube were provided as shelter. Individuals were thereafter released into 14 patches (August). Each patch was connected to two other patches (an empty patch and another occupied patch) by two twin corridor systems as described in the Results. The corridors had low light penetration precluding thermoregulation, and they therefore represented a hostile habitat for lizards. We thus excluded the possibility of lizards traveling through these corridors as part of their routine daily movements. Lizards traveling through these corridors were caught in a 30-cm-deep pitfall trap at the end of the corridor and released into the patch they were moving toward. Dispersal was monitored from August until the end of October and from March to April (winter months were excluded because of the hibernation of this species). Checking of pitfall traps was always performed using the same protocol to limit the impact of the experimenter. The lizards captured in the pitfall traps were considered 'dispersers', whereas those remaining in their release patch were considered 'residents'. The length of the dispersal corridors corresponds to the distance covered by dispersers in nature¹⁸. Individuals covering such distances in nature have been defined as dispersers because they very rarely return (2% of all movements)²⁹. In June 2011, all surviving lizards were recaptured during ten successive sessions (hand recaptures). Given the high cumulative capture rate (98%; ref. 18), noncaptured lizards were considered dead. Surviving females were housed in individual terrariums under standardized conditions until they gave birth.

Ethical issues have been supervised by a local committee of Toulouse University.

Butterfly experiment *P. brassicae* caterpillars originated from Ariège (France) and were reared in climatic chambers at 23 °C under photoperiodic conditions (light:dark 14:10 h) with food provided *ad libitum*. Butterflies were marked individually, kept in the lab and fed with flowers until sufficient numbers of individuals for the Metatron experiment were produced. Emerging butterflies were then released 1 d after emergence into the Metatron over four sessions between 15 and 23 September 2010. The first release

session of 120 butterflies was followed by three more releases over 2 weeks to maintain a constant density in the patches. The experiment ended with the death of the last butterfly. A total of 211 butterflies, 113 females and 98 males, were released at the center of eight patches, each of which was connected to a single empty patch by a single corridor. Individuals could therefore stay in the release patch or cross the corridor to the empty patch. Within each patch, feeding flower pots and host plant pots were placed in the same position to ensure favorable life conditions. The position of each individual in the system was then recorded during capture sessions performed twice a day. Each individual was released at the point of capture. In total, 29 capture sessions were performed over 28 experimental days. As with the lizard experiment, capture sessions were always performed using the same protocol within each patch to limit the experimenter impact. It is noteworthy that this protocol corresponds exactly to the one used during field investigations of butterfly metapopulation dynamics³⁰. Survival and capture probabilities were estimated using MARK³¹ under the Cormack-Jolly-Seber Model. The general model included both time and sex effects with their interaction. The relevance of the inclusion of each parameter was assessed by using the Akaike information criterion (AIC). The best model was selected in cases where ΔAIC with the second-best model was <2 . Minimal survival was estimated for each individual as the number of days from emergence to the last capture. To determine the impact of the time spent in the laboratory before release on survival, we performed a linear model using the R software v.2.12.1. Data were log transformed to achieve normality.

'Dispersers' were defined as individuals that entered a corridor at least once, whereas 'residents' were defined as individuals that stayed in the release patch throughout their lifetime (excluding individuals never captured after their first release session); that is, dispersers and residents were defined in the same manner as for the lizard experiments. Successive crossings were defined as each reverse movement in the system: from the corridor to the release patch, from the empty patch to the corridor or from the empty patch to the release patch. Host plants were checked daily for the presence of egg clutches. Each egg clutch was brought to the laboratory until hatching, and caterpillars were reared in the same conditions as their parents until emergence.

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